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American Philosophical Society

Held at Philadelphia for Promoting Useful Knowledge

VOLUME 86, NUMBER 3 JULY 8, 1943

PAPERS

on

ASTRONOMY, BOTANY, GEOLOGY, PALEONTOLOGY, AND ZOOLOGY

PHILADELPHIA
THE AMERICAN PHILOSOPHICAL SOCIETY
INDEPENDENCE SQUARE
1943

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LANCASTER PRESS, INC., LANCASTER, PA.

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VARIABLE STARS AND THE SOURCES OF STELLAR ENERGY

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(*Read April 24, 1942*)

ABSTRACT

The variable stars occupy an important position relative to the stars in general. They are one of the most important sources of information concerning stellar dimensions and constitution, and among them are found the extremes in observed luminosities, masses, and temperatures. They are therefore vital test objects for theories of stellar interiors, such as the theory of the energy sources of the stars with which the present paper is concerned.

The first purpose of the paper is to present the summarized results of a study of the physical dimensions of variable stars. The stellar model that is most appropriate for the discussion of these data is next considered. Finally the material is applied to a consideration of the central temperatures of the stars.

All the central temperatures for *intrinsic* variables are found to be too low for the operation of the "carbon cycle." It is shown that, on the assumptions made as to models, the several types of intrinsic variables, and even the progression of properties within any one type, may be individually related to the subatomic processes depending on lithium, beryllium, and boron.

Most of the eclipsing stars, on the other hand, fall in the domain where the "carbon cycle" is supposed to be operative.

During the past few years a quantitative theory of the role played by nuclear processes in supplying the sources for stellar energy has been developed by Bethe (1939). The more successful applications of the theory have been to the main-sequence or "dwarf" stars; the "giant" stars present a different problem, which has been discussed by Bethe and Marshak (1939), by Gamow (1939), by Gamow and Teller (1939), and by Greenfield (1941). The variable stars are of paramount importance in the study of giant stars, and therefore it has seemed worth while to rediscuss them with especial reference to their fundamental physical dimensions. Our extensive observational attack on the brighter variable stars, outlined by C. Payne-Gaposchkin (1939), is providing new determinations of some basic relationships.

PHYSICAL DIMENSIONS OF VARIABLE STARS

An extensive discussion of the observed material for variable stars is in preparation and will be published elsewhere; here it will be necessary only to tabulate the physical parameters and indicate the source of the information for each type of intrinsic variable. The significant relationships are the period-luminosity relation, the spectrum-luminosity relation, the period-spectrum relation, and the scale of effective temperatures. For purposes of discussion the variable stars are classified as Cepheid variables, long-period variables, and semiregular red variables. The tabular entries are computational quantities, and the number of significant figures is accordingly greater than the precision of the data warrants.

1. *Cepheid Variables.*—The first table summarizes the period-spectrum relation and the scale of effective temperatures for Cepheid variables; the first is taken from Payne-Gaposchkin and Gaposchkin (1938), and the second is deduced from the discussion of the stellar temperature scale by Kuiper (1938). Table 2 gives the period-luminosity relation, as revised by Shapley (1940), and the absolute bolometric magnitude derived by means of table 1 with the aid of Kuiper's *empirical* table of bolometric corrections to the visual magnitudes of giant stars (Kuiper, 1938) and our investigation of the color indices of giant stars (Payne-Gaposchkin, 1935). Table 3 gives the three fundamental parameters, luminosity, radius, and mass, expressed as logarithms with the solar dimensions as unit. The luminosity, L, is calculated from the relation

$$\log L = 0.4(4.85 - M)$$

where M is the absolute bolometric magnitude of the star, 4.85 is the adopted absolute bolometric magnitude of the sun. The radius, R, is calculated from the relation

$$2 \log R = \log L - \log \pi ac - 4 \log T_e \quad (1)$$

TABLE 1

CEPHEID VARIABLES: PERIOD, SPECTRUM, AND EFFECTIVE TEMPERATURE

Logarithm of Period in Days	Median Spectrum	Logarithm of Effective Temperature in Degrees K.	Logarithm of Period in Days	Median Spectrum	Logarithm of Effective Temperature in Degrees K.
−0.6	A3	3.959	0.8	G2	3.703
−0.4	A6.5	3.914	1.0	G4	3.681
−0.2	A9	3.886	1.2	G5.5	3.663
0.0	F2	3.851	1.4	G7	3.648
0.2	F4	3.820	1.6	G9	3.623
0.4	F7	3.778	1.8	K0	3.613
0.6	F9	3.748	2.0	K1	3.602

TABLE 2

CEPHEID VARIABLES: PERIOD AND LUMINOSITY

Logarithm of Period in Days	Absolute Photographic Magnitude	Absolute Bolometric Magnitude	Logarithm of Period in Days	Absolute Photographic Magnitude	Absolute Bolometric Magnitude
−0.6	0.00	−0.24	0.8	−1.66	−3.19
−0.4	0.00	−0.42	1.0	−2.02	−3.68
−0.2	−0.07	−0.60	1.2	−2.39	−4.19
0.0	−0.31	−0.97	1.4	−2.80	−4.64
0.2	−0.68	−1.48	1.6	−3.25	−5.29
0.4	−1.01	−2.09	1.8	−3.73	−5.86
0.6	−1.33	−2.61	2.0	−4.24	−6.56

where a, the coefficient of Stefan's law, is 7.64×10^{-15}, c, the velocity of light, is 3×10^{10} cm/sec, and T_e is the effective temperature as given in table 1. The mass, M, is taken, throughout this paper, from the empirical mass-luminosity relation as tabulated by Kuiper (1939). No direct determinations of the masses of variable stars are available (with a few important exceptions, such as VV Cephei), and in the present stage of investigation it may be profitable to explore the consequences of supposing that their masses are normal for their luminosities. Small deviations from the mass-luminosity relation would leave the main physical features unchanged.

The material of table 3 is somewhat similar to that compiled and discussed by Beileke (1937), and the results of the discussion are closely accordant. In his table of radii (table 11) Beileke gives, as the "probable value" of the radius, 9.5 for $\log P = 0.2$, and 263 for $\log P = 1.70$. If allowance is made for the fact that he has assumed a value of 0.05 for the zero-point of the period-luminosity curve, instead of 0.00 as given in table 2, and for slight differences in his adopted period-spectrum relation and scale of effective temperatures, the two sets of material are effectively equivalent.

2. *Long-period Variables.*—The next three tables summarize for the long-period variables the period-spectrum relation and the scale of effective temperatures; the spectrum-luminosity relation; and the luminosities, radii, and masses. The period-spectrum relation is from Payne-Gaposchkin and Gaposchkin (1938); the scale of effective temperatures has been deduced from the data and discussions of Pettit and Nicholson (1921 and 1933) and the work of Gabovitz and Öpik (1935) and of Gabovitz (1936) on the coloring effect of titanium oxide. The spectrum-luminosity relation for the long-period variables of spectrum M has been deduced with the aid of the investigations of Wilson (1923, 1939*a*, and 1941) and is in good accordance with the recent work of Wilson and Merrill (1942), which was kindly made available to us before publication. For the N stars, the data of table 4 rest on unpublished discussions; those of table 5 depend

TABLE 3

CEPHEID VARIABLES: LUMINOSITY, RADIUS, AND MASS (SOLAR UNITS)

Logarithm of Period in Days	Logarithm of Luminosity	Logarithm of Radius	Logarithm of Mass	Logarithm of Period in Days	Logarithm of Luminosity	Logarithm of Radius	Logarithm of Mass
−0.6	2.04	0.64	0.64	0.8	3.22	1.63	0.99
−0.4	2.11	0.74	0.66	1.0	3.41	1.78	1.05
−0.2	2.18	0.83	0.68	1.2	3.62	1.91	1.12
0.0	2.33	0.96	0.73	1.4	3.80	2.05	1.17
0.2	2.53	1.12	0.78	1.6	4.06	2.22	1.26
0.4	2.78	1.29	0.86	1.8	4.28	2.35	1.35
0.6	2.98	1.44	0.92	2.0	4.56	2.49	1.43

TABLE 4

LONG-PERIOD VARIABLES: SPECTRUM, PERIOD, AND EFFECTIVE TEMPERATURE

Maximum Spectrum	Logarithm of Period in Days	Logarithm of Effective Temperature in Degrees K.	Maximum Spectrum	Logarithm of Period in Days	Logarithm of Effective Temperature in Degrees K.
K5e	1.99	3.61:	M7e	2.60	3.437
M0e	2.07	3.595:	M8e	2.68	3.410
M1e	2.14	3.580			
M2e	2.22	3.558	R8e	2.41	3.462
M3e	2.30	3.535	N0e	2.51	3.442
M4e	2.37	3.514	N2e	2.59	3.422
M5e	2.45	3.490	N4e	2.68	3.402
M6e	2.52	3.462	N6e	2.77	3.382

TABLE 5

LONG-PERIOD VARIABLES: SPECTRUM AND LUMINOSITY

Maximum Spectrum	Absolute Visual Magnitude	Absolute Bolometric Magnitude	Maximum Spectrum	Absolute Visual Magnitude	Absolute Bolometric Magnitude
K5e	−1.9	−3.35	M7e	+0.2	−4.6:
M0e	−2.3	−3.85	M8e	+0.3	−5.0:
M1e	−2.7	−4.42			
M2e	−2.3	−4.25	R8e	−1.70	−3.20
M3e	−1.8	−4.06	N0e	−1.15	−3.55
M4e	−1.2	−3.92	N2e	−0.70	−4.10
M5e	−0.6	−4.0:	N4e	−0.25	−4.35
M6e	0.0	−4.3:	N6e	+0.25	−4.45

TABLE 6

LONG-PERIOD VARIABLES: LUMINOSITY, RADIUS, AND MASS (SOLAR UNITS)

Maximum Spectrum	Logarithm of Luminosity	Logarithm of Radius	Logarithm of Mass	Maximum Spectrum	Logarithm of Luminosity	Logarithm of Radius	Logarithm of Mass
K5e	3.28	1.94	1.02	M7e	3.78	2.53	1.18
M0e	3.48	2.07	1.09	M8e	3.93	2.66	1.23
M1e	3.71	2.22	1.16				
M2e	3.64	2.22	1.14	R8e	3.22	2.13	1.01
M3e	3.56	2.26	1.11	N0e	3.36	2.34	1.05
M4e	3.49	2.24	1.10	N2e	3.58	2.57	1.12
M5e	3.54	2.31	1.11	N4e	3.68	2.70	1.15
M6e	3.65	2.43	1.13	N6e	3.72	2.76	1.16

on the work of Wilson (1939*b*). The absolute bolometric magnitudes depend on newly determined bolometric corrections—mere estimates for the N stars, reposing upon reasoning similar to that used by Gabovitz and Öpik for the M stars.

3. *The Semiregular Variables.*—The least-investigated of the intrinsic variables are the stars of small range and erratic behavior that may be called the semiregular variables, though all the evidence now tends to suggest that they are doubly regular rather than "half-regular." Several studies have recently converged on this interesting group. Joy (1940) and Keenan (1942) have made important studies of their spectra, and the data now given are deduced from an extensive unpublished study of the light variations, made at the Harvard Observatory, with important assistance from Keenan's paper, which was kindly made available before publication.

Table 7 gives the period-spectrum relation and scale of effective temperatures. The M stars

TABLE 7

SEMIREGULAR RED VARIABLES: SPECTRUM, PERIOD, AND EFFECTIVE TEMPERATURE

Maximum Spectrum	Logarithm of Period in Days	Logarithm of Effective Temperature in Degrees K.	Maximum Spectrum	Logarithm of Period in Days	Logarithm of Effective Temperature in Degrees K.
M0	1.64	3.535	c M0	2.0	3.535
M1	1.75	3.522	c M1	2.2	3.522
M2	1.86	3.507	c M2	2.4	3.507
M3	1.97	3.490	c M3	2.6	3.490
M4	2.08	3.465			
M5	2.19	3.438	R8	1.95	3.462
M6	2.30	3.406	N0	2.13	3.442
M7	2.41	3.370	N2	2.29	3.422
M8	2.52	3.330	N4	2.44	3.402
M9	2.63	3.290:	N6	2.61	3.382

are subdivided into normal stars and supergiants on the basis of Keenan's luminosity classification; the presence of supergiants in the group was also mentioned by Joy (1940). Table 8 gives the adopted spectrum-luminosity relation—a very rough approximation, probably correct only in the mean. Table 9 contains the luminosities, radii, and masses. The data for the semiregular variables are less certain than those for long-period variables, and those for long-period variables are less reliable than those of Cepheids. However, all the quantities tabulated are undoubtedly of the right order.

4. *The Eclipsing Variables.*—A second source of basic data is furnished by the eclipsing stars and double stars. Compilations of data for these groups, in a form suitable for the present appli-

TABLE 8

SEMIREGULAR RED VARIABLES: SPECTRUM AND LUMINOSITY

Maximum Spectrum	Absolute Visual Magnitude	Absolute Bolometric Magnitude	Maximum Spectrum	Absolute Visual Magnitude	Absolute Bolometric Magnitude
M0	0.30	−1.25	c M0	−5.2	−6.8
M1	0.30	−1.42	c M1	−5.2	−7.0
M2	0.30	−1.65	c M2	−5.2	−7.2
M3	0.30	−1.96	c M3	−5.2	−8.5
M4	0.30	−2.42			
M5	0.30	−3.1:	R8	−0.75	−2.25
M6	0.30	−3.4:	N0	−0.75	−3.15
M7	0.30	−3.7:	N2	−0.75	−4.15
M8	0.30	−4.1:	N4	−0.30	−4.40
M9	0.30	−4.5:	N6	+0.10	−4.60

TABLE 9

SEMIREGULAR RED VARIABLES: LUMINOSITY, RADIUS, AND MASS (SOLAR UNITS)

Maximum Spectrum	Logarithm of Luminosity	Logarithm of Radius	Logarithm of Mass	Maximum Spectrum	Logarithm of Luminosity	Logarithm of Radius	Logarithm of Mass
M0	2.22	1.56	0.69	c M0	4.66	2.78	1.46
M1	2.26	1.60	0.71	c M1	4.74	2.85	1.48
M2	2.38	1.69	0.74	c M2	4.82	2.92	1.51
M3	2.54	1.81	0.79	c M3	5.34	3.21	1.69
M4	2.82	2.00	0.88				
M5	3.18	2.24	0.99	R8	2.84	2.02	0.88
M6	3.50	2.46	1.09	N0	3.22	2.25	1.00
M7	3.98	2.77	1.24	N2	3.62	2.49	1.12
M8	4.70	3.21	1.47	N4	3.70	2.57	1.16
M9	5.30	3.59	1.66	N6	3.78	2.60	1.18

cation, have been published by Gaposchkin (1939, 1940).

CONSTITUTION OF INTRINSIC VARIABLES

In order to pass from observed data to internal conditions, it is necessary to come to some conclusions as to the constitution of the stars considered. If the star is built on any polytropic model, the polytropic index can be inferred from the central condensation. In the case of a pulsating star, the polytropic index may be found by an application of the pulsation theory.

The central condensation, for a star of mass M, luminosity L, and radius R, may be calculated if the mean molecular weight μ and the hydrogen content X_0 are known. In the present application we adopt the value 1.00 for the mean molecular weight, whence, since $\mu = 2/(1 + 3X_0)$, the hydrogen content is 0.33. The central condensation is given by Chandrasekhar (1939) as a function of the quantities α and f, which (with the adopted values of μ and X_0) are given by:

$$\log \alpha = -2.229 + \tfrac{1}{4}(2 \log L + \log R - 3 \log M),$$

$$\log f = -1.234 + \tfrac{1}{2}(\log L + \tfrac{1}{2} \log R - 5.5 \log M).$$

These formulae may be used directly with the data contained in tables 3, 6, and 9. The values of the central condensation, ξ^*, are then deduced graphically from the tables given by Chandrasekhar. If the stars are polytropes, the polytropic index, n, follows directly from the value of ξ^*. The values of ξ^* and the corresponding values of n are given in table 10.

TABLE 10

CENTRAL CONDENSATION AND POLYTROPIC INDEX FOR INTRINSIC VARIABLES

CEPHEIDS			LONG-PERIOD VARIABLES			SEMIREGULAR VARIABLES		
Logarithm of Period	ξ^*	n	Maximum Spectrum	ξ^*	n	Maximum Spectrum	ξ^*	n
−0.6	0.580	2.6	K5e	0.498	3.0	M0	0.470	3.1
−0.4	0.525	2.8	M0e	0.497	3.0	M1	0.475	3.1
−0.2	0.524	2.8	M1e	0.495	3.0	M2	0.469	3.1
0.0	0.522	2.9	M2e	0.492	3.0	M3	0.470	3.1
0.2	0.517	2.9	M3e	0.476	3.1	M4	0.477	3.1
0.4	0.522	2.9	M4e	0.459	3.2	M5	0.457	3.2
0.6	0.525	2.8	M5e	0.461	3.2	M6	0.442	3.3
0.8	0.508	3.0	M6e	0.439	3.3	M7	0.397	3.5
1.0	0.516	2.9	M7e	0.439	3.3	M8	0.27:	4.0:
1.2	0.509	3.0	M8e	0.420	3.4	Mean		3.19
1.4	0.480	3.1	Mean		3.15			
1.6	0.460	3.2	R8e	0.482	3.1	R8	0.463	3.2
1.8	0.460	3.2	N0e	0.455	3.2	N0	0.457	3.3
2.0	0.430	3.3	N2e	0.428	3.3	N2	0.431	3.3
Mean		2.96	N4e	0.413	3.4	N4	0.431	3.3
			N6e	0.398	3.5	N6	0.420	3.4
			Mean		3.30	Mean		3.30

The group of high-luminosity semiregular variables gives results that are far more uncertain, because the luminosities given by Keenan are subject to some revision, and because the temperatures of the supergiant M stars, and consequently their radii, are uncertain. They lead to an average polytropic index of about 3.8.

It is seen from the fundamental formulae that the determinations of ξ^* and n are most sensitive to the mass, less to the luminosity, and least to the radius. In our data, luminosity and radius are rather certain, but mass has been determined

from luminosity on the basis of the empirical mass-luminosity relation. If variable stars are under-luminous (that is, if their masses are higher than we have assumed for a given luminosity), both α and f will be reduced, and in consequence, ξ^* will be increased and the polytropic index reduced. If, on the other hand, they are over-luminous, the polytropic indices will be greater than those in table 10. There are few definite deviations from the mass-luminosity relation (other than the white dwarfs and the Trumpler stars, both classes of objects widely different from the intrinsic variables in all physical properties) and even for these the deviations are small. There is no reason to doubt that the results of table 10 are of the right order, if the basic assumptions are admitted.

It is seen that the average polytropic index is about 3. If the hydrogen content is larger than we have assumed, and the mean molecular weight therefore smaller, the polytropic index for a given star is smaller. For example, if X_0 is 0.8, μ is 0.58, and for semiregular variables of spectrum M5, ξ^* is 0.57, and n is 2.7, instead of 3.2 as given in the table for the adopted conditions. It is very unlikely that the mean molecular weight is larger than our adopted value of 1.00, so that larger values of n for this reason are not to be expected. A value of a little over 3 seems to represent all the data; no significance is now attached to the suggestion shown that n tends to increase with advancing type.

Another method of deducing the polytropic index, by an application of the pulsation theory, has been given by Miller (1929). His formulae for n, when the conditions of our problem are inserted, reduce to:

$$n = 4.32(-0.465 - \log P - \tfrac{1}{2}\log \rho) \quad (2)$$

where ρ is the mean density of the star, which is readily calculable from our data. The values of n that are derived from our data by Miller's method are given in table 11.

An approximate method of determining the period of radial pulsation of a star has been given by Ledoux and Pekeris (1941):

$$\sigma_0^2 = \frac{-(3\Gamma_1 - 4)\Omega}{I}$$

where $\sigma_0 = 2\pi/P$, Γ_1 is the effective ratio of specific heats, Ω the gravitational potential, and I the moment of inertia. Results are given for four values of polytropic index. Applications of this formula duplicate the results of table 11, if the same value (1.429) for the effective ratio of the specific heats is used as was used in the application of the Miller formula. This relatively low value of Γ_1 has been considered probable for intrinsic variables since Eddington (1926: 194) first introduced it for Cepheids; and Cowling (1935) has linked a small value of the quantity (less than 1.44) with the instability of Cepheid variables that finds expression in their pulsations.

The mean polytropic indices for stars of several types from the two main methods (central concentration and pulsation theory) are summarized in table 12.

Thus for the intrinsic variables the standard model ($n = 3$) seems to be a useful assumption. It has been pointed out, however, by Chandrasekhar (1938: 318) that there is a breakdown

TABLE 11

POLYTROPIC INDICES FROM THE PULSATION THEORY

CEPHEIDS				LONG-PERIOD VARIABLES				SEMIREGULAR VARIABLES			
log P	n	log P	n	Spectrum	n	Spectrum	n	Spectrum	n	Spectrum	n
−0.6	3.0	1.0	2.6	K5e	1.9	R8e	0.9	M0	1.2	R8	2.5
−0.4	2.8	1.2	2.4	M0e	2.0	N0e	1.7	M1	1.0	N0	2.9
−0.2	2.4	1.4	2.4	M1e	2.6	N2e	2.7	M2	1.0	N2	3.5
0.0	2.3	1.6	2.4	M2e	2.2	N4e	3.1	M3	1.2	N4	3.3
0.2	2.4	1.8	2.2	M3e	2.2	N6e	3.1	M4	1.7	N6	2.7
0.4	2.4	2.0	2.1	M4e	1.6	Mean	2.30	M5	2.6	Mean	2.98
0.6	2.4	Mean	2.47	M5e	1.7			M6	3.3		
0.8	2.6			M6e	2.1			M7	(4.5)		
				M7e	2.3			M8	(6.2)		
				M8e	2.7			Mean	2.54		
				Mean	2.12						

TABLE 12

COMPARISON OF POLYTROPIC INDICES

Type of Variable	Central Condensation	Pulsation Theory
Cepheids	2.96	2.47
Long-period M	3.15	2.12
Long-period N	3.30	2.30
Semiregular M	3.19	2.54
Semiregular N	3.30	2.98
Mean	3.18	2.48

of the standard model for the massive supergiants, such as the M component of VV Cephei, which is actually one of the semiregular red variables, classed by Keenan (1942) with the highly luminous group. Therefore it seems probable that the best available model for the study of these luminous red stars is the point-source model, discussed by Chandrasekhar (1938). The outer parts of stars with this model correspond to $n = 3.25$, the central regions to polytropic cores with $n = 1.5$ (Chandrasekhar, 1939: 172). The central condensation method gives a value near to the former; the pulsation-theory determination lies closer to the value 1.5.

It should be pointed out that these conclusions depend on the observed physical dimensions of the stars, and it is of interest to consider how they would be affected if these physical dimensions were altered. Accordingly the absolute visual and absolute bolometric magnitudes have been computed from Miller's formula for a star of 300 days' period, and for a number of different polytropic indices. The results are given in table 13. The likely absolute visual magnitudes all fall between $n = 1$ and $n = 3.5$.

CENTRAL TEMPERATURES OF VARIABLE STARS

The central temperatures will now be deduced on the basis of three formulae: for the standard model, with the adopted conditions as to μ and X_0:

$$\log T_c = 7.2949 + \log (\mu\beta M/R)$$

(Chandrasekhar, 1938: 230), where β is the ratio of gas pressure to total pressure. For the point-source model, with radiation-pressure neglected, we have:

$$\log T_c = 7.3175 + \log (M/R)$$

(Chandrasekhar, 1938: 351). The minimum temperature, irrespective of model, is given by Chandrasekhar (1939*b*) as:

$$T_{c,\,min} = 11.54 Q_{min} \mu (M/R) \times 10^6,$$

Q_{min} being a quantity tabulated as a function of mass and radiation-pressure. The three formulae probably cover the likely range of central temperature, unless some radically different type of model should be considered.

The central temperatures deduced for the several types of variable stars on the basis of the three formulae quoted are contained in table 14.

As an indication of the dependence on n of the central temperature, and therefore of the possible latitude in the interpretation of central temperatures, the calculations have been made for the semiregular variables of spectrum M5 with several polytropic indices. The formula is:

$$T_c = \frac{R' G \mu \beta M}{(n+1) M' \mathfrak{R} R}$$

as given by Eddington (1926: 85), who defines the constants. The results of the calculation are given in table 15. The table shows that the central temperatures are lower than the "standard-model" temperatures, when n is greater than 3.

ENERGY SOURCES FOR VARIABLE STARS

The data of table 14 lead to the conclusion that the central temperatures of almost all the intrinsic variable stars considered are less than ten million degrees, and those of the long-period and semiregular variables are less than three million degrees. It follows that the carbon-cycle, discussed by Bethe (1939) as the source of energy for the stars of the main sequence, cannot be contemplated as the source of energy of the

TABLE 13

DEPENDENCE OF ABSOLUTE VISUAL MAGNITUDE ON POLYTROPIC INDEX (PERIOD 300 DAYS)

Polytropic Index	1	2	3	4	4.5	4.9
Logarithm of Mean Density (cgs)	−6.33	−6.80	−7.26	−7.72	−7.95	−8.14
Absolute Bolometric Magnitude	−3.00	−4.00	−5.00	−5.90	−6.40	−6.80
Absolute Visual Magnitude	−0.25	−1.25	−2.25	−3.15	−3.65	−4.05

TABLE 14

CENTRAL TEMPERATURES OF VARIABLE STARS (UNIT 1,000,000° K.)

CEPHEID VARIABLES				LONG-PERIOD VARIABLES				SEMIREGULAR VARIABLES			
Logarithm of Period	Standard Model	Point-Source Model	Minimum	Maximum Spectrum	Standard Model	Point-Source Model	Minimum	Maximum Spectrum	Standard Model	Point-Source Model	Minimum
−0.6	13.8	20.9	6.8	K5e	1.26	2.51	0.71	M0	1.78	2.82	0.91
−0.4	11.5	17.4	5.6	M0e	1.17	2.34	0.66	M1	1.70	2.69	0.85
−0.2	9.6	14.8	4.8	M1e	1.10	2.19	0.62	M2	1.45	2.34	0.74
0.0	7.6	12.3	3.9	M2e	1.00	2.00	0.56	M3	1.17	2.00	0.62
0.2	5.6	9.6	3.0	M3e	0.81	1.66	0.46	M4	0.87	1.58	0.48
0.4	4.3	7.8	2.3	M4e	0.74	1.55	0.42	M5	0.58	1.17	0.34
0.6	3.4	6.3	1.9	M5e	0.60	1.32	0.36	M6	0.42	0.71	0.24
0.8	2.4	4.8	1.4	M6e	0.47	1.05	0.28	M7	0.25	0.62	0.15
1.0	1.9	3.9	1.1	M7e	0.38	0.93	0.23	M8	0.11	0.38	0.07
1.2	1.5	3.4	0.89	M8e	0.31	0.78	0.19	M9	0.06	0.24	0.04
1.4	1.2	2.8	0.71								
1.6	0.89	2.3	0.55	R8e	0.79	1.58	0.45	R8	0.83	1.51	0.46
1.8	0.72	2.1	0.46	N0e	0.51	1.07	0.30	N0	0.58	1.17	0.33
2.0	0.58	1.8	0.37	N2e	0.33	0.74	0.20	N2	0.40	0.89	0.23
				N4e	0.26	0.59	0.15	N4	0.35	0.81	0.21
				N6e	0.22	0.53	0.14	N6	0.33	0.79	0.20

TABLE 15

CENTRAL TEMPERATURE AND POLYTROPIC INDEX FOR SEMIREGULAR VARIABLE, SPECTRUM M5

Polytropic Index	0.5	1.0	1.5	2.0	2.5	3.0	4.0	4.5	4.9
Logarithm of Central Temperature	5.52	5.54	5.57	5.62	5.69	5.77	6.06	6.37	7.06

intrinsic variables (unless, as stated earlier, very different stellar models than the ones we have considered are to be used). The alternative of the lithium-beryllium-boron processes as the sources of energy of these variables seems at present the most promising, as has been shown by Gamow (1938 and 1939), Gamow and Teller (1939), and Greenfield (1941).

The derivation of the energy of the intrinsic variables from nuclear transmutations involving the lighter atoms (lithium to boron) implies that the already elapsed life of these stars (*as such*) is short—about 10^8 years—compared to the probable lifetime of stars like the sun (10^{10} years). This has been used by some as an argument against the dependence on these processes, and hence against such central temperatures and stellar models as we have used. However, recent work of Spitzer (1941) and Whipple (1942) has tended to remove the difficulty, by showing that the formation of stars from interstellar dust clouds is a current possibility, and that the available supply of pre-stellar material is adequate.

The central temperatures of the intrinsic variables, as indicated by the point-source and standard-model formulae, depend essentially on the ratio of mass to radius, M/R. The dependence of M/R on absolute bolometric magnitude is shown in the figure, where log (M/R) is plotted against absolute bolometric magnitude. In addition to the intrinsic variables, a selected list of eclipsing stars (table 16) for which good photometric and spectroscopic data are available, has been entered in the diagram; components of one system are connected by straight lines. The brighter component is always the more massive. Table 16 also contains data for the sun; for Capella; the sub-dwarf eclipsing system UX Ursae Majoris; the components of the visual binary Krüger 60; a faint M dwarf; bright non-variable stars in two globular clusters as published by Shapley (1930); and a mean for the long-period variables in the globular cluster 47 Tucanae, as given by Shapley (1941).

Ordinates in the figure are absolute bolometric magnitudes; abscissae are logarithms of M/R (solar units). Below the figure are indicated the logarithms of the corresponding central temperatures *calculated on the point-source model*, and the central temperatures themselves. These temperatures apply only to the stars for which the point-source model is applicable (the intrinsic

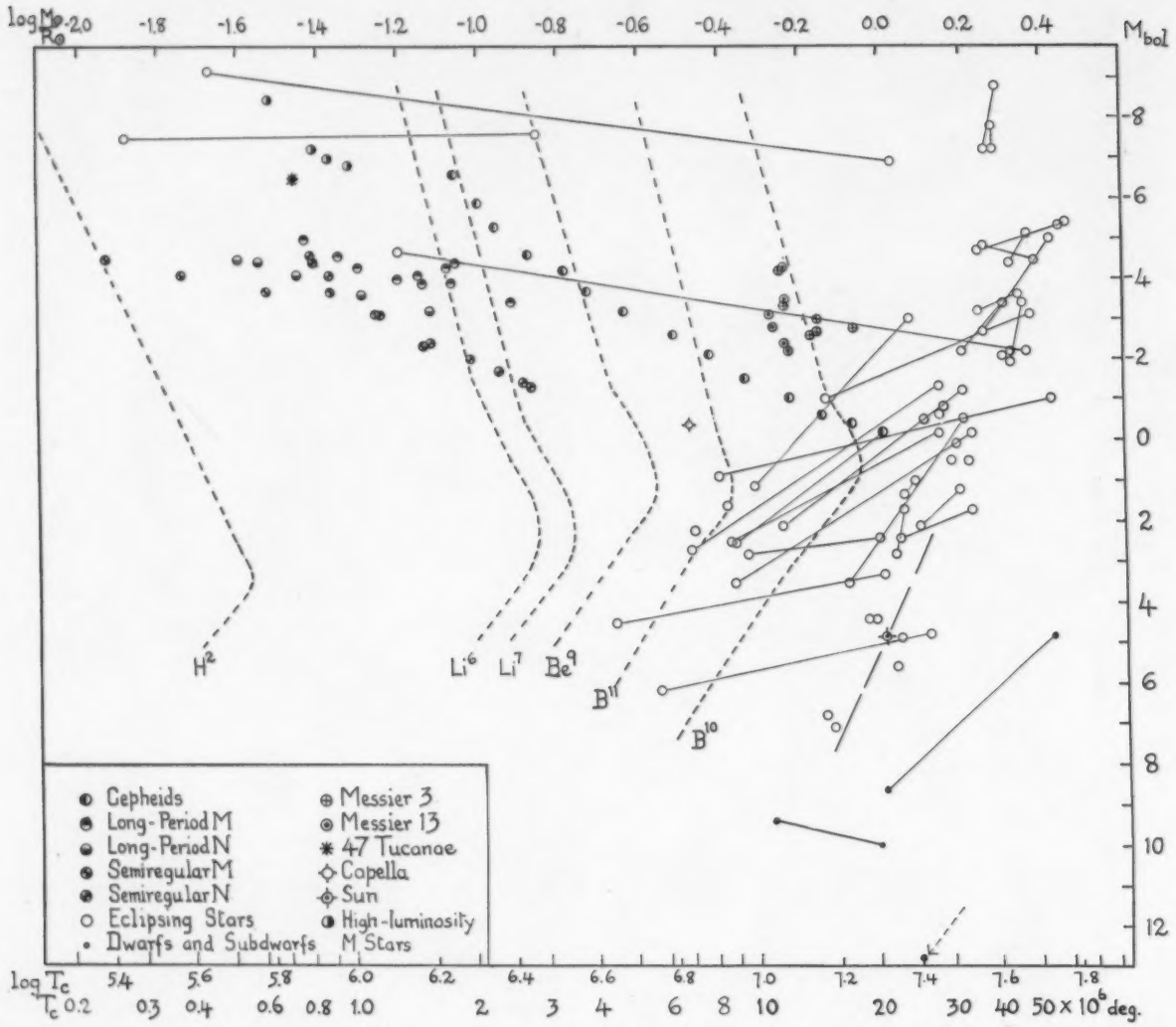

FIG. 1. Logarithm of M/R (solar units) plotted against absolute bolometric magnitude, for stars indicated at lower left. Below are indicated central temperatures (point-source model only). "Conflict lines" for various subatomic processes are inserted as broken lines.

variables, on our assumption). The "point-source" temperature is higher than the "standard-model" temperature which has usually been considered to represent the main-sequence stars.

Calculations by Greenfield (1941) have related the dimensions of the stars to the subatomic processes supplying their energy. The "conflict lines" given in his paper have been transferred to our diagram, where the atom responsible for the energy production under the conditions concerned is marked.

It is seen that (as already pointed out by Greenfield) different types of variable stars seem to be associated with different subatomic processes. No variable stars are seen to be associated with deuterium; lithium operates for the semiregular and long-period variable stars (and possibly the two forms of lithium may be associated with the two types of long-period variables that correspond to two maxima of period-frequency). The Cepheids span three subatomic processes, and these seem to divide them into the same three groups that the progression in form of light curve has already indicated (Gaposchkin, 1938). It seems that all intrinsic variables fall within the domain of the lithium-beryllium-boron processes, if our data have correctly reproduced their physical properties.

TABLE 16

MASSES AND RADII OF ECLIPSING VARIABLES

Star	First Component			Second Component		
	Absolute Bolometric Magnitude	Logarithm of Mass	Logarithm of Radius	Absolute Bolometric Magnitude	Logarithm of Mass	Logarithm of Radius
S Ant	1.67	0.37	0.32	2.77	0.23	0.20
σ Aql	−1.21	0.73	0.53	−0.80	0.68	0.53
TT Aur	−3.39	1.00	0.70	−2.20	0.85	0.65
WW Aur	0.95	0.48	0.40	1.26	0.43	0.38
AR Aur	0.46	0.52	0.31	0.53	0.51	0.34
β Aur	−0.50	0.64	0.54	−0.50	0.64	0.54
ε Aur	−7.58	1.52	2.37	−7.47	1.51	3.37
ζ Aur	−4.66	1.16	2.36	−2.25	0.86	0.50
i Boo	5.61	−0.13	−0.16	5.61	−0.13	−0.16
RS CVn	3.30	0.16	0.16	4.54	0.01	0.68
UW CMa	−7.81	1.55	1.27	−7.20	1.47	1.19
TV Cas	−0.58	0.65	0.51	2.11	0.31	0.56
AO Cas	−8.82	1.68	1.39	−7.15	1.47	1.21
U Cep	−0.24	0.60	0.44	2.46	0.27	0.65
VV Cep	−9.16	1.72	3.39	−6.86	1.42	1.39
AH Cep	−5.26	1.23	0.79	−4.66	1.16	0.92
U CrB	−0.97	0.70	0.28	0.93	0.46	0.87
Y Cyg	−5.35	1.24	0.78	−5.35	1.24	0.78
GO Cyg	−0.49	0.64	0.44	3.50	0.11	0.20
MR Cyg	−0.20	0.60	0.60	2.52	0.32	0.70
YY Gem	6.81	−0.28	−0.13	7.10	−0.31	−0.18
Z Her	2.40	0.28	0.29	2.81	0.22	0.56
RX Her	0.09	0.56	0.38	0.09	0.56	0.38
TX Her	1.22	0.42	0.23	2.08	0.32	0.23
u Her	−4.76	1.17	0.92	−4.54	1.14	0.76
RT Lac	1.64	0.37	0.76	2.25	0.29	0.76
AR Lac	4.81	−0.03	−0.14	6.25	−0.21	0.35
CM Lac	1.66	0.37	0.15	2.39	0.28	0.24
U Oph	−2.23	0.85	0.53	−2.06	0.83	0.53
WZ Oph	4.35	0.03	0.05	4.42	0.02	0.06
AG Per	−3.42	1.00	0.65	−1.92	0.82	0.50
V Pup	−5.06	1.21	0.85	−4.45	1.13	0.81
U Sge	−1.34	0.74	0.60	2.74	0.23	0.71
μ^1 Sco	−3.58	1.02	0.68	−3.17	0.97	0.73
W UMa	4.89	−0.04	−0.08	4.89	−0.04	−0.08
TX UMa	−0.25	0.61	0.39	3.50	0.14	0.51
UX UMa	4.82	−0.03	−0.45	8.58	−0.50	−0.50
Z Vul	−3.11	0.96	0.59	−0.97	0.70	0.84
RS Vul	−2.95	0.94	0.87	1.12	0.44	0.72
HV 11111	−5.00	1.41	0.99	−2.69	1.01	0.76
Krüger 60	10.0	−0.78	−0.76	9.4	−0.60	−0.32
Sun	4.85	0.00	0.00			
Capella	−0.4	0.62	1.14			
Cluster Giants (Mean)	−3.2	1.00	1.22			
47 Tuc (Mean)	−6.5	1.42	2.88			
Dwarf M	12.8	−1.00	−1.08			

A number of the eclipsing stars are seen to fall within the same domain. Among these, the brighter components of VV Cephei, ζ Aurigae, and ε Aurigae are known intrinsic variables, and almost all the others within the domain (being the fainter components of eclipsing systems) might be slightly variable without having been detected. The rare yellow giants, such as Capella, also fall within the domain. There is here a suggestion that the tendency to variability is associated with the process of energy-generation. It is noteworthy that the M and N stars, which are distinguished by differences of composition (carbon and nitrogen and oxygen) show no differentiation of properties in the figure.

The stars to the right in the figure are "main-sequence" stars which, according to current theory, are fed by the "carbon-cycle." The line drawn through the point indicating the sun indicates the place where the carbon-cycle is effective. In several cases the figure would suggest different energy-sources for the two components of eclipsing stars. The interesting evolutionary problems that are suggested by the figure are beyond the scope of the present paper.

The writers take pleasure in thanking Dr. Chandrasekhar for his advice and counsel.

REFERENCES

BEILEKE, F. 1937. *Zeitschr. f. Astrophys.* **14**: 1.
BETHE, H. A. 1939. *Phys. Rev.* **55**: 434.
BETHE, H. A., AND R. E. MARSHAK. 1939. *Report on progress in Physics* **6**: 1.
CHANDRASEKHAR, S. 1939. Introduction to the study of stellar structure. Chicago.
—— 1939*a*. *Proc. Am. Philos. Soc.* **81** (2).
—— 1939*b*. *Royal Astron. Soc. Monthly Notices* **99**: 673.
COWLING, T. G. 1936. *Royal Astron. Soc. Monthly Notices* **96**: 42.
EDDINGTON, A. S. 1926. The internal constitution of the stars. Cambridge.
GABOVITZ, J. 1936. *Tartu Publ.* **28** (5).
GABOVITZ, J., AND E. ÖPIK. 1935. *Tartu Publ.* **28** (3).
GAMOW, G. 1939. *Phys. Rev.* **55**: 718, 796.
GAMOW, G., AND E. TELLER. 1939. *Phys. Rev.* **55**: 791.
GAPOSCHKIN, S. 1938. *Proc. Nat. Acad. Sci.* **24**: 1.
—— 1939. *Jour. Royal Astron. Soc. Canada* **33**: 233.
—— 1940. *Proc. Am. Philos. Soc.* **82** (3).
GREENFIELD, M. A. 1941. *Phys. Rev.* **60**: 175.
JOY, A. H. 1941. Symposium on variable stars. Am. Astron. Soc., 1941.
KEENAN, P. C. 1942. *Astrophys. Jour.*, in press.
KUIPER, G. 1939. *Astrophys. Jour.* **88**: 429.
LEDOUX, P., AND C. L. PEKERIS. 1941. *Astrophys. Jour.* **94**: 124.
MILLER, J. C. P. 1929. *Royal Astron. Soc. Monthly Notices* **90**: 64.
PARENAGO, P. 1940. *Publ. Sternberg State Astron. Inst.* **13**, part 1: 59.
PAYNE-GAPOSCHKIN, C. 1935. *Harvard Ann.* **89** (6): 109.

—— 1939. *Proc. Am. Philos. Soc.* **81**: 189.
PAYNE-GAPOSCHKIN, C., AND S. GAPOSCHKIN, 1938. Variable stars. Harvard Observatory Monograph 5.
PETTIT, E., AND S. B. NICHOLSON. 1929. *Astrophys. Jour.* **68**: 279.
—— 1933. *Astrophys. Jour.* **78**: 320.
SHAPLEY, H. 1930. Star clusters. Harvard Observatory Monograph 2.
—— 1940. *Proc. Nat. Acad. Sci.* **26**: 541.
SPITZER, L. 1941*a*. *Astrophys. Jour.* **93**: 369.
—— 1941*b*. *Astrophys. Jour.* **94**: 232.
WHIPPLE, F. L. 1942. Paper presented at the Inter-American Astrophysical Congress, Tonanzintla, Mexico, February, 1942.
WILSON, R. E. 1923. *Astron. Jour.* **35**: 125.
—— 1939*a*. *Astron. Jour.* **48**: 37.
—— 1939*b*. *Astrophys. Jour.* **90**: 352, 486.
—— 1941. *Publ. Astron. Soc. Pacific* **53**: 227.
WILSON, R. E., AND P. W. MERRILL. 1942. *Astrophys. Jour.* **95**: 248.

THORIUM IN THE SUN

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ABSTRACT

A paper recently published on the Zeeman Effect of *Th* II has stimulated further study on the question of *Th* in the sun. One of the authors, A. S. King, at Mount Wilson, has photographed the laboratory spectra of *Th* I and of *Th* II and has estimated intensities of the conspicuous low-temperature lines.

On the basis of this material there is no evidence of the presence of *Th* I in the sun. For *Th* II, the *raie ultime*, λ4019, is probably present but faint in the solar spectrum. One other line of *Th* II, λ7525, may also possibly be present.

The total number of elements identified in the sun is now 66. Of these, 4 are identified somewhat dubiously. For 6 elements no statement can be made because of insufficient laboratory data. Twenty elements are absent from the sun.

IN 1939, at a symposium of the American Philosophical Society on "Progress in Astrophysics," a paper was presented by one of the present authors (C. M. S.), entitled "The Composition of the Sun." In this paper a summary of elements in the sun listed 64 present, 2 with insufficient solar data, 7 with insufficient laboratory data, and 19 absent. Since then more work has been done on the subject, and it is now possible to revise that summary, with special regard to thorium.

Lists of the leading lines of *Th* I and *Th* II were published by Mark Fred in 1938.[1] At that time a search for this element in the sun was made, but for two reasons no conclusion could be drawn. First, a compressed intensity scale was used. While the leading low-temperature lines could be selected, the strongest were not conspicuous, as for example, the *raie ultime*. Second, the separation of *Th* I and *Th* II lines needed to be checked carefully by further experimental work in the laboratory.

Fortunately, this latter task was undertaken at the Massachusetts Institute of Technology, where films of the Zeeman Effect of *Th* II were made, with the use of the powerful Bitter magnet. The Zeeman patterns separate *Th* I and *Th* II lines conclusively. A preliminary analysis of the *Th* II spectrum, giving the Zeeman Effect data, was recently published by J. Rand McNally, Jr., George R. Harrison, and Helen B. Park.[2] From this paper one can select those lines of *Th* II arising from the lowest state of the atom, for which resolved Zeeman patterns were obtained.

Here again the intensities of the lines were not primarily investigated. Further laboratory experiments were needed to select the most persistent lines. One of the present authors, A. S. King, of the Mount Wilson Observatory, undertook this task. His electric-furnace plates show the strongest low-level lines of *Th* I and *Th* II, and his estimated intensities show the differences among the strong lines.

TABLE 1

STRONGEST LINES OF *Th* I

LABORATORY			SUN				
I A (MIT)	Intensity		I A	Intensity		Δλ (⊙-Lab)	Solar Ident.
	Arc	Furnace		Disk	Spot		
5760.554	150	200	.538	−2	−2	−016	
4493.340	100	150	.381	−1	0	+041	−Cr?
3719.436	100	80	.460	−2N	−	+024	Gd^{+}?

The data for *Th* I are entered in table 1. The successive columns of the table contain the laboratory wave-lengths, King's estimated arc and furnace intensities, the nearest solar wave-length, the solar disk and spot intensities, Δλ (sun-laboratory), and the solar identifications. There are three conspicuous lines. This spectrum has not yet been analyzed, but the furnace intensities indicate that these are the strong low-temperature lines. Consequently, if *Th* I is present in the sun, they are the lines to be expected. They should be strengthened in the spot spectrum, where less ionization occurs than in the disk spectrum. The strongest of the three, λ5760, agrees fairly well in wave-length with a solar line, but this is *not* strengthened in

[1] *Astrophys. Jour.*, **87**: 176, 1938.

[2] *Jour. Opt. Soc. America*, **32**: 334, 1942.

the spot spectrum. The $\Delta\lambda$ for the second line, λ4493, is too large to be permitted. The discordance in wave-length of the third line is not serious, and the spot spectrum has not been observed to the violet of λ3894; but it is unlikely that only the weakest of the three is present. The existing evidence is, therefore, fairly conclusive that *Th* I is absent from the sun.

The analysis of the spectrum of *Th* II and King's estimated intensities provide us with valuable criteria on which to judge whether or not this element is present. The lower excitation potential, *i.e.* the amount of energy required to raise an atom to the state where it can absorb a line, can be calculated when the spectroscopic terms are known. If any lines are present, the strongest lines having the lowest excitation potentials should be found in the solar spectrum. In table 2 the data for *Th* II are listed under the two headings, "Laboratory" and "Sun" as above. The first column contains the laboratory wave-length; the second, King's estimated arc and furnace intensities; the third, the lower excitation potential; and the fourth, the multiplet designation. On the right-hand side of the table the solar data are arranged as in table 1. The excitation potentials in parentheses are not on the same scale as the others, and probably are higher by an appreciable fraction of a volt.

Two facts are conspicuous in this table. First, the strongest low-level line, and the one which was originally suspected as the *raie ultime*, λ4019, fits an otherwise unidentified solar line. (A weak line of *Co* I was originally assigned dubiously to this solar line. Owing to the faintness of the *Co* line, the behavior of the rest of the lines in its multiplet, and its comparatively high excitation potential (2.27 volts), it was rejected from the solar spectrum before the question of *Th* II arose.) Second, the weaker low-level *Th* II lines are not present. If the *raie ultime* produces only a faint solar line, it is not surprising that these lines are absent.

King lists the line at λ7525 as twice as strong as λ5989. This line may be present in the sun, but the identification is subject to some question, since the excitation potential of the line is not known. Furthermore, the solar identifications in the red are not yet definitive, and other attempts to identify the solar line should be made before it is assigned to *Th* II.

One may, therefore, conclude from this evidence that the *raie ultime* of *Th* II, λ4019, is present in the solar spectrum, and that thorium occurs in the sun only in the ionized state.

The table of "Elements in the Sun" should now be revised as shown in table 3. A total of 66 may be called present. Of this number, the evidence for the four in parentheses is somewhat dubious. There are still insufficient laboratory data for 6 elements. Two elements, *Ne* and *Cs*, were formerly classed as having insufficient solar data. Since there is no evidence of their presence, they are here included among those listed as absent, making the total in this class 20. The absent elements are arranged, as before, in three groups. In the first two groups the excitation potential of the accessible lines is entered above the chemical symbol. The elements in the first of these three

TABLE 2

STRONGEST LINES OF *Th* II

LABORATORY					SUN				
I A	Intensity		Lower E P	Multiplet Designation	I A	Intensity		$\Delta\lambda$ ⊙-lab	Solar Ident.
	Arc	Furnace				Disk	Spot		
7525.52	500	—	—	—	.50	−3d?		−02	Th^+?
5989.035	250	—	0.19	$a^4F_{2\frac{1}{2}}-z^2D^0_{1\frac{1}{2}}$	absent				
5049.810	200	—	(0.27)	$(a^4F^0_{1\frac{1}{2}}-z^4G_{2\frac{1}{2}})$	.829	6	6	+019	Fe
4919.814	500	1?	(0.21)	$(a^4H^0_{3\frac{1}{2}}-z^4G_{2\frac{1}{2}})$	absent				
4391.114	600	10	(0.00)	$(a^2F^0_{2\frac{1}{2}}-z^4G_{3\frac{1}{2}})$	.149	−2		+035	
4277.322	400	10	0.00	$a^4F_{1\frac{1}{2}}-y^2P^0_{1\frac{1}{2}}$	absent				
4019.137	1500	40	0.00	$a^4F_{1\frac{1}{2}}-y^2F^0_{2\frac{1}{2}}$	.140	−1		+003	Th^+
3539.589	400	10	0.00	$a^4F_{1\frac{1}{2}}-z^4F^0_{2\frac{1}{2}}$	absent				
3392.040	300	10	0.19	$a^4F_{2\frac{1}{2}}-y^2G^0_{3\frac{1}{2}}$	.018	1		−022	Fe
3180.199	400	10	0.19	$a^4F_{2\frac{1}{2}}-z^4F^0_{3\frac{1}{2}}$	.237	3		+038	Fe

TABLE 3

ELEMENTS IN THE SUN

Present	66	H	He	Li	Be	B	C	N	O	F	Na	Mg	Al	Si
		P	S	K	Ca	Sc	Ti	V	Cr	Mn	Fe	Co	Ni	Cu
		Zn	Ga	Ge	Rb	Sr	Y	Zr	Cb	Mo	Ru	Rh	Pd	Ag
		Cd	In	(Sn)	Sb	Ba	La	Ce	Pr	Nd	Sm	Eu	Gd	(Tb)
		Dy	Er	Tu	Yb	Lu	Hf	(Ta)	W	Os	Ir(Au)	Pt	Pb	Th
Insufficient laboratory data	6	Ma	Il	Ho	85	87	U							
Absent	20													
Ultimate lines accessible	4	0.0	0.0	0.0	0.0	0.0								
		Cs	Re	Tl	Bi	Ra*								
Ultimate lines inaccessible	11	2.3	4.9	5.5	6.0	6.9								
		As	Hg	Te	Se	I								
		7.8	8.3	8.9	9.9	11.5	16.6							
		Br	Xe	Cl	Kr	A	Ne							
Not to be expected	5	Po	Rn	Ra	Ac	Pa								

* Entered twice.

groups could certainly be detected in the sun if present in quantities comparable with any of those which have been found. The high excitation potentials of the accessible lines are unfavorable for the detection of those in the second group. Those in the last group are radioactive and are of relatively short life.

The writers are greatly indebted to Mr. Henry Norris Russell not only for suggesting this paper but also for his helpful advice and keen interest. The larger subject of solar identifications in general is one on which the Princeton and Mount Wilson Observatories have been collaborating for several years.

AN APPLICATION OF THE METHOD OF LEAST SQUARES TO THE ADJUSTMENT OF PHOTOMETRIC ELEMENTS OF ECLIPSING BINARIES

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ABSTRACT

In the first part of this paper equations are set up for a least-squares adjustment of photometric elements of eclipsing binaries which consist of two spherical components revolving in circular orbits. The coefficients of the differential corrections for uniform as well as darkened disks are evaluated in a closed form for every type of eclipse, and expressed in terms of functions that are already familiar in the theory of light curves of close eclipsing systems. It is pointed out (part II) that, in practical cases, the numerical values of coefficients of the individual corrections can be conveniently obtained from tabular differences of existing tables of the "uniform" and "darkened" α-functions. In part III applications to AR Cassiopeiae and α Coronae borealis are carried out as illustrative examples, with special respect to the determination of their limb darkening. Stebbins' elements of these variables are completely confirmed and their probable errors are obtained. The bright B3-component of AR Cas is found to be very little darkened at limb ($u = 0.00 \pm 0.04$, p.e.) in the blue ($\lambda = 4500$ A); while the darkening of Gemma (class A0) at the same effective wave length proves to be conspicuous.

1.—In discussions of photometric measures of eclipsing variables the first aim of a computer should be to derive a set of photometric elements of the eclipse and to compare the resulting theoretical light curve with the observations. If the curve is found systematically to deviate from the observed normals, the preliminary elements are evidently in need of an adjustment. This can be done by several methods, among which an application of the principles of least squares holds a prominent place. For not only do we obtain in this way the most probable values of the individual elements, but also the uncertainty with which these elements are specified by the photometric material. A knowledge of errors of definitive photometric elements should in general be regarded as important as knowledge of the elements themselves; and consequently no orbital solution should be regarded as complete unless its errors have at least been approximated.

An application of least squares to an adjustment of photometric elements of eclipsing binaries is not new, though it has never been used extensively. First attempts in this direction are due to Myers[1] and Roberts[2] as early as at the end of the nineteenth century. Fifteen years later the procedure was revived by Russell and Shapley[3] in their study of Z Draconis; while in 1937 Pannekoek and Miss van Dien[4] worked out an application of least squares by way of variation of constants. All these investigations were, however, insufficiently general from the present point of view (that is, their authors attempted to adjust only certain elements or certain auxiliary constants) and are of a mainly historical interest today. The first modern investigation, in which all elements involved were equally subject to an appropriate adjustment, is that by Wyse.[5] In his study the geometry of the problem was, however, solved in a finite number of terms only for uniformly bright disks; while the case of limb-darkened disks, not tractable in terms of elementary functions, was dealt with only by approximate methods. The present formulation of the problem is novel and is believed to be considerably simpler. In contrast to Wyse's, it will permit an equal treatment of partial eclipses irrespective of whether it is the smaller or the larger star which gets eclipsed; and it leads to all results expressed in a closed form and in terms of functions that are already familiar in the theory of light curves of close eclipsing systems.

I. EQUATIONS OF THE PROBLEM

2.—Of the various forms of application of least squares to the present problem, an adjustment of preliminary elements by way of differential corrections appears to be the most general and efficient, and admits of an elegant and simple mathematical formulation. Let, as usual, L_1 denote the fractional light of the component

[1] *Illinois Observ. Bull.* 1, 1898.
[2] *Royal Astron. Soc. Monthly Notices* **63**: 527, 1903.
[3] *Astrophys. Jour.* **39**: 405, 1914.
[4] *Bull. Astron. Inst. Netherlands* **8**: 141, 1937.
[5] *Lick Observ. Bull.* 494, 1939.

undergoing eclipse (the combined light of the system taken as unity) and f be the fractional loss of light at any moment within eclipse. The corresponding fractional light l of the whole system then becomes

$$l = 1 - fL_1. \tag{1}$$

If both components can be regarded as spherical and the distribution of brightness over the apparent disk of the eclipsed star is governed by limb-darkening alone, then, as is well-known,

$$f = \frac{3(1-u)}{3-u} f^U + \frac{2u}{3-u} f^D, \tag{2}$$

where u is the coefficient of darkening of the star undergoing eclipse, and f^U, f^D stand for the fractional losses of light if the eclipsed disk were uniformly bright ($u = 0$) or completely darkened at limb ($u = 1$). Let, further, r_1, r_2 denote the fractional radii of the eclipsed and eclipsing star, respectively, and δ, the apparent separation of their centers. If the relative orbit of both components is regarded as circular and its apparent radius is taken as the unity of length, then

$$\delta^2 = \sin^2 \psi \sin^2 i + \cos^2 i,$$

where ψ denotes the true anomaly (phase angle) of the eclipsing component in the relative orbit (measured from the moment of maximum eclipse), and i is the inclination of the orbital plane to the celestial sphere. If, finally,

$$s = \frac{r_1^2 - r_2^2 + \delta^2}{2\delta},$$

then, so long as the eclipse is partial,

$$\pi r_1^2 f^U = \left\{ \int_s^{r_1} \int_{-\sqrt{r_1^2-x^2}}^{+\sqrt{r_1^2-x^2}} + \int_{\delta-r_2}^{s} \int_{-\sqrt{r_2^2-(\delta-x)^2}}^{+\sqrt{r_2^2-(\delta-x)^2}} \right\} dxdy, \tag{3.0}$$

and

$$\frac{2}{3}\pi r_1^3 f^D = \left\{ \int_s^{r_1} \int_{-\sqrt{r_1^2-x^2}}^{+\sqrt{r_1^2-x^2}} + \int_{\delta-r_2}^{s} \int_{-\sqrt{r_2^2-(\delta-x)^2}}^{+\sqrt{r_2^2-(\delta-x)^2}} \right\} \sqrt{r_1^2 - x^2 - y^2}\, dxdy, \tag{3.1}$$

regardless of whether the eclipsed component is the larger or the smaller of the two. If, however, the eclipse becomes annular, the first double integral in curly brackets on the right-hand sides of (3.0) or (3.1) is to be dropped, and the upper limit of integration with respect to x becomes $\delta + r_2$ instead of s.

Symbolically, therefore,

$$f = f(\delta, r_1, r_2, u) \quad \text{or} \quad f(\psi, i, r_1, r_2, u).$$

It may be assumed that the time of minimum and the phase angle ψ corresponding to each observation are so accurately known as to require no subsequent corrections, and that approximate values of r_1, r_2, and i have been derived by elementary methods for an assumed value of u. Let, further, Δl denote the residuals between light observed at any particular moment and predicted by means of the approximate elements. Each normal observed within minima then supplies us with an equation of the form

$$\Delta l = -f\Delta L_1 - L_1 \Delta f, \tag{4.0}$$

where

$$\Delta f = \frac{\partial f}{\partial r_1}\Delta r_1 + \frac{\partial f}{\partial r_2}\Delta r_2 + \frac{\partial f}{\partial i}\Delta i + \frac{\partial f}{\partial u}\Delta u, \tag{4.1}$$

and the symbols ΔL_1, Δr_1, Δr_2, Δi, and Δu stand for values of the differential corrections which are to be added algebraically to the respective elements in order to obtain their improved values. As many equations of the form (4) are available as there are observed normals. Provided that their number sufficiently exceeds the number of quantities sought for, a least-squares solution of such a set of equations then yields the most probable values of required corrections as well as their errors. A basic feature of our present problem is, however, that unlike in certain other astronomical applications (proper motions, parallax determination), the coefficients of the differential corrections are not constant, but depend upon provisional values of elements which we seek to improve. Therefore, in order to be able to set up the equations of condition, an explicit knowledge of the partial derivatives of f with respect to the elements involved and for every type of eclipse is prerequisite. The whole complexity of the present problem centers around the formation of these derivatives.

3.—Of the four coefficients involved in (4.1), that of u presents the least difficulty; for differentiating (2) we get at once

$$\frac{\partial f}{\partial u} = 6\,\frac{f^D - f^U}{(3-u)^2}. \tag{5}$$

The remaining three partial derivatives can be obtained either by differentiation of the explicit formulae for f or, more conveniently, by differentiating equations (3) behind the integral sign. Not all three coefficients need be obtained by direct differentiation, however. Since, by definition, f is a function not of r_1, r_2, and δ independently, but only of their ratios, the partial derivatives of f with respect to these elements must satisfy the relation

$$r_1\frac{\partial f}{\partial r_1} + r_2\frac{\partial f}{\partial r_2} + \delta\frac{\partial f}{\partial \delta} = 0. \tag{6}$$

Of these three derivatives, $\partial f/\partial r_2$ can be anticipated to be the simplest and $\partial f/\partial r_1$ the most complex one. In what follows we propose, therefore, to evaluate the derivatives with respect to r_2 and δ directly and then to obtain $\partial f/\partial r_1$ by means of (6). Differentiating equations (3), we find that

$$\left.\begin{aligned} \frac{\partial f^U}{\partial r_2} &= +2\,\frac{r_2}{r_1^2}\,I^0_{-1,0}, & \frac{\partial f^D}{\partial r_2} &= +3\,\frac{r_2^2}{r_1^3}\,I^0_{-1,1},\\ \frac{\partial f^U}{\partial \delta} &= -2\,\frac{r_2}{r_1^2}\,I^1_{-1,0}, & \frac{\partial f^D}{\partial \delta} &= -3\,\frac{r_2^2}{r_1^3}\,I^1_{-1,1}, \end{aligned}\right\} \tag{7}$$

where

$$\pi r_2^{\beta+\gamma+m+1} I^m_{\beta,\gamma} = \int_{\delta-r_2}^{c} [r_2^2 - (\delta - x)^2]^{\beta/2} \times [2\delta(s-x)]^{\gamma/2}[\delta - x]^m dx, \tag{8}$$

and $c = s$ or $\delta + r_2$ as to whether the eclipse is partial or annular. The remaining derivatives then follow from

$$\frac{\partial f}{\partial r_1} = -\frac{r_2}{r_1}\frac{\partial f}{\partial r_2} - \frac{\delta}{r_1}\frac{\partial f}{\partial \delta} \tag{9}$$

and

$$\frac{\partial f}{\partial i} = \frac{\partial f}{\partial \delta}\frac{\partial \delta}{\partial i} = -\frac{1}{\delta}\frac{\partial f}{\partial \delta}\sin i\cos i\cos^2\psi. \tag{10}$$

The above-defined functions of the form $I^m_{\beta,\gamma}$ are not unfamiliar in the theory of light curves of eclipsing binary systems. The same functions were found to specify also the photometric effects of rotational and tidal distortion of the eclipsing component;[6] and their general solution was already investigated by the writer[7] so that only the pertinent results may be presently recalled. It can be established[7] that

$$\left.\begin{aligned} I^0_{-1,0} &= \frac{\cos^{-1}\mu}{\pi},\\ I^0_{-1,1} &= \frac{2}{\pi}\sqrt{\frac{\delta}{r_2}}\,\{2E - (1+\mu)F\},\\ I^1_{-1,0} &= \frac{1}{\pi}\sqrt{1-\mu^2},\\ I^1_{-1,1} &= \frac{2}{3\pi}\sqrt{\frac{\delta}{r_2}}\,\{(1+\mu)F - 2\mu E\}, \end{aligned}\right\} \tag{11.0}$$

if the eclipse is partial, and

$$\left.\begin{aligned} I^0_{-1,0} &= 1, & I^0_{-1,1} &= \frac{4}{\pi\kappa}\sqrt{\frac{\delta}{r_2}}\,E,\\ I^1_{-1,0} &= 0, & & \\ I^1_{-1,1} &= \frac{4}{3\pi\kappa}\sqrt{\frac{\delta}{r_2}}\,\{(1+\mu)F - \mu E\}, \end{aligned}\right\} \tag{11.1}$$

if it is annular. In these equations

$$\mu = \frac{\delta - s}{r_2} = \frac{r_2^2 - r_1^2 + \delta^2}{2\delta r_2},$$

while F and E stand for the Legendre complete elliptic integrals of the first and second kind, with the modulus

$$\kappa^2 = \frac{1}{2}(1-\mu)$$

if the eclipse is partial, and

$$\kappa^2 = \frac{2}{1-\mu}$$

if it is annular. These two moduli are evidently reciprocal.

The functions $I^m_{\beta,\gamma}$ as defined by equation (8) are positive dimensionless quantities which could be tabulated in terms of suitable parameters, such as μ and δ/r_2 or, more generally, the ratio of radii and the geometrical depth of the eclipse. Once this has been done, the evaluation of the coefficients of equation (4) in terms of provisional

[6] Kopal, *Proc. Am. Philos. Soc.* **85**: 399, 1942 (*cf.* also *Astrophys. Jour.* **94**: 159, 1941).

[7] *Op. cit.*, section VI (21).

elements will be reduced to a trivial task. It is to be hoped that such tables will be constructed soon—especially in view of the fact that the same tables are also required for the evaluation of photometric elements of distortion of the eclipsing star. At present, however, the $I^{m}{}_{\beta,\gamma}$'s are not yet available in tabular form; and the question arises as to whether the computation of partial derivatives of f may be facilitated by the use of the existing tables of "uniform" or "darkened" α-functions. As will be shown below, the answer is in the affirmative; and the procedure itself proves of sufficient interest to be developed in some detail.

II. Evaluation of Derivatives in Terms of the α-Functions

4.—Let α denote, as usual, the fractional loss of light, during eclipse, of a uniformly bright disk (α^U) or one that is completely darkened at limb (α^D). The unit in which the α's are conventionally expressed is the loss of light that would take place at the moment of internal tangency. If the eclipsed star is the smaller of the two, the moment of internal tangency coincides with the beginning of totality and the light lost then equals the whole luminosity of the eclipsed star. If, on the other hand, the latter is the larger of the two, only a fraction q of its light gets lost at the moment of internal tangency. The α-functions so normalized vary from zero at the beginning of the eclipse to unity at the moment of internal tangency regardless of the type of eclipse.

The loss of light of the whole system within minima continues to be given by equation (1); but f rewritten in terms of the α-functions assumes different forms if the star undergoing eclipse is the smaller of the two than if it is the larger. If we put, for brevity's sake,

$$\frac{2u}{3-u} = x$$

then during eclipse of the smaller star (occultation)

$$f_a = (1 - x_a)\alpha^U + x_a\alpha_a{}^D, \qquad (12.0)$$

while if the reverse is the case (transit)

$$f_b = (1 - x_b)q^U\alpha^U + x_bq^D\alpha_b{}^D. \qquad (12.1)$$

In these equations $x_{a,b}$ pertain to the darkening of the smaller or larger component, respectively, while $\alpha^D{}_{a,b}$ denote the fractional "darkened" losses of light during occultation or transit.[8] Equation (12.1) holds good for partial and annular phase of a transit as well; in the latter case merely $\alpha^U = 1$ while $\alpha_b{}^D > 1$.

Equations (12) differentiated with respect to u yield

$$\frac{\partial f_a}{\partial u_a} = 6\frac{\alpha_a{}^D - \alpha^U}{(3-u_a)^2}$$

and (13)

$$\frac{\partial f}{\partial u_b} = 6\frac{q^D\alpha_b{}^D - q^U\alpha^U}{(3-u_b)^2},$$

in agreement with (5); while the derivatives of f with respect to the remaining elements can be obtained as follows. Let r_a, r_b denote the fractional radii of the smaller and the larger component, respectively (regardless of which one of the two undergoes eclipse), and i, as before, the orbital inclination. If, for brevity's sake, w stands for either of these then, evidently,

$$\frac{\partial f_a}{\partial w} = (1 - x_a)\frac{\partial \alpha^U}{\partial w} + x_a\frac{\partial \alpha_a{}^D}{\partial w} \qquad (14.0)$$

and

$$\frac{\partial f_b}{\partial w} = (1 - x_b)\left\{\alpha^U\frac{\partial q^U}{\partial w} + q^U\frac{\partial \alpha^U}{\partial w}\right\} + x_b\left\{\alpha_b{}^D\frac{\partial q^D}{\partial w} + q^D\frac{\partial \alpha_b{}^D}{\partial w}\right\}. \qquad (14.1)$$

Now it can be established that $q^U = k^2$, while[9]

$$q^D = \frac{2}{\pi}\left\{\sin^{-1}\sqrt{k} + \frac{1}{3}(4k-3)(2k+1)\sqrt{k(1-k)}\right\}, \qquad (15)$$

where k, the ratio of the radii, is defined, as usual, by r_a/r_b. The only derivatives of q^U which are not identically zero are

$$\frac{\partial q^U}{\partial r_a} = \frac{2}{r_b}k \quad \text{and} \quad \frac{\partial q^D}{\partial r_b} = -\frac{2}{r_b}k^2. \qquad (16)$$

In differentiating q^D we find it convenient to put

$$\frac{\partial q^D}{\partial w} = \frac{\partial q^D}{\partial k}\frac{\partial k}{\partial w}. \qquad (17)$$

Since from (15) we obtain

$$\frac{\partial q^D}{\partial k} = \frac{16}{\pi}k\sqrt{k(1-k)}, \qquad (18)$$

[8] In terms of notations employed by Russell and Shapley $\alpha_a{}^D = \alpha'$ and $\alpha_b{}^D = \alpha''$.

[9] *Cf.*, for instance, Kopal, *Astrophys. Jour.* **94**: 145 (sec. 7), 1941.

the only non-zero derivatives of q^D are again found to be

$$\frac{\partial q^D}{\partial r_a} = \frac{16k}{\pi r_b}\sqrt{k(1-k)}$$

and (19)

$$\frac{\partial q^D}{\partial r_b} = -\frac{16k^2}{\pi r_b}\sqrt{k(1-k)}.$$

The derivatives of the α-functions with respect to the geometrical elements are generally complex. In practice, however, their direct computation can be avoided. It is well known that all α-functions can be made to depend on two parameters—such as the ratio of the radii k and the geometrical depth of the eclipse p—the latter defined, as usual,

$$p = \frac{\delta - r_b}{r_a}.$$

We are therefore entitled to put

$$\frac{\partial \alpha}{\partial w} = \frac{\partial \alpha}{\partial k}\frac{\partial k}{\partial w} + \frac{\partial \alpha}{\partial p}\frac{\partial p}{\partial w}. \tag{20}$$

This substitution separates terms depending on properties of each individual system and those which are purely geometrical. For only the derivatives of k and p with respect to r_a, r_b, and i need be computed anew for each particular star; and these are, fortunately, simple; namely

$$\frac{\partial k}{\partial r_1} = \frac{1}{r_b}, \qquad \frac{\partial k}{\partial r_b} = -\frac{k}{r_b}, \qquad \frac{\partial k}{\partial i} = 0, \tag{21}$$

and

$$\frac{\partial p}{\partial r_a} = -\frac{p}{r_a}, \qquad \frac{\partial p}{\partial r_b} = -\frac{1}{r_a},$$
$$\frac{\partial p}{\partial i} = \frac{1}{r_a}\frac{\partial \delta}{\partial i} = -\frac{\sin^2 i}{2\delta r_a}\cos^2\psi. \tag{22}$$

Of these derivatives, only $\partial p/\partial r_a$ and $\partial p/\partial i$ are found to vary with the phase; the rest are constant for each particular system. Inserting (21) and (22) in (20), we then obtain

$$\frac{\partial \alpha}{\partial r_a} = \frac{1}{r_b}\frac{\partial \alpha}{\partial k} - \frac{p}{r_a}\frac{\partial \alpha}{\partial p}, \tag{23.0}$$

$$\frac{\partial \alpha}{\partial r_b} = -\frac{k}{r_b}\frac{\partial \alpha}{\partial k} - \frac{1}{r_a}\frac{\partial \alpha}{\partial p}, \tag{23.1}$$

$$\frac{\partial \alpha}{\partial i} = -\sin 2i\,\frac{\cos\psi}{2\delta r_a}\frac{\partial \alpha}{\partial p}. \tag{23.2}$$

The derivatives of α with respect to k and p are again functions of k and p only and could therefore be tabulated in terms of these parameters once for all. In practice, however, this seems hardly expedient; for the numerical value of the derivatives can be readily extracted from tabular differences of the respective α-tables. Extensive 5-figure tables of α^U, $\alpha_a{}^D$, and $\alpha_b{}^D$, recently published by Zessewitsch,[10] should be ample for this purpose. With the use of (16), (19), and (23) it is easy to evaluate the coefficients of the differential corrections by means of equations (14), and a least-squares solution of a set of properly weighted equations of condition then yields the values of corrections to the individual elements required to make the sum of squares of the residuals Δl a minimum.

5.—The foregoing method permits a completely simultaneous treatment of the primary and secondary minima and is subject to very few limitations. There are some, however. The most obvious one is related to the fact that the coefficients of the differential corrections in equation (4) are not constant, but are functions of the elements we seek to improve. Hence if the corrections to one or more elements exceed their probable errors by an order of magnitude, the original equations of condition are no longer sufficiently accurate. The coefficients in (4) should then be recomputed with the use of the improved elements, a new set of equations should be solved, and this procedure should be repeated until the resulting corrections are no longer significant. The convergence of such approximations depends upon the geometry of each particular case. It is likely to be more rapid in case of an occultation than of a transit. But it is evident that if the initial residuals Δl are large or obviously systematic, the labor of constructing and solving successive sets of the equations of condition may become considerable. Only after a really good fit has been obtained by cruder but more flexible procedures (such as the method of false position, or arbitrary variation of constants), is it justifiable, and in fact indispensable, to apply the least squares.

Secondly, the method as developed so far takes no account of the fact that, in certain cases, the errors of individual elements may be correlated.[11] As an example we may recall[9] that, for shallow partial eclipses, the sum of the radii $r_a + r_b$ is much more determinate from photometric data than their ratio r_a/r_b. Should the

[10] *Bull. Astron. Inst. Leningrad* 45, 1939, and 50, 1940.

[11] Or, in other words, that the conventional photometric elements r_a, r_b, and i may not be the best quantities to be solved for directly from photometric material.

present method be applied to such a system, the errors of r_a and r_b would undoubtedly come out large; but the fact that their sum can be obtained with much greater weight would remain concealed. A refinement of the present method to incorporate constraints imposed by the geometry of eclipses remains still a task for the future.

An inspection of the order of magnitude of coefficients of the differential corrections in equation (4) reveals a good deal regarding the determinacy of the individual elements. In particular, we note that whereas the partial derivatives of f with respect to r_a, r_b, and i (except for the latter in the neighborhood of $i = 90°$) are generally quantities of the order of magnitude zero or one-tenth, that with respect to u (proportional to the difference $\alpha^D - \alpha^U$) is as a rule of the order of one-hundredth or less. This fully exposes the difficulty experienced in determining the values of the coefficient of limb-darkening simultaneously with other geometrical elements; and at the same time makes it evident that any determinations of u without simultaneous adjustment of r_a, r_b, and i would have very little meaning—at least as long as observations in only one frequency of light are available. The same applies to the determination of uncertainty in orbital inclination if the eclipse is nearly central; for if $i \to 90°$, $\partial f/\partial i$ also goes to zero.

In order to carry out a simultaneous adjustment of all the elements, accurate observational data as well as favorable geometrical circumstances are necessary. With respect to u, the weight of a solution for Δu—small as it is—becomes the greater, the greater the average value of $\partial f/\partial u$. The conditions are found to become optimal if

(*a*) the eclipse is annular,
(*b*) the eclipse is central and both components are nearly of the same size.

The likelihood of eclipses of the latter type is small, and their solution leaves again Δi largely undetermined; but systems with $k \ll 1$ exhibiting annular eclipses are not quite as rare. It is on such systems that the attention of observers aiming at a determination of darkening has been primarily concentrated. As an example, we may recall a pioneer investigation of YZ Cassiopeiae by Wyse and Kron[12] in which the authors succeeded in determining the coefficient of darkening of the principal component of this eclipsing system with a probable error not exceeding 8 percent. In what follows we are going to carry out a similar analysis for two other eclipsing binaries exhibiting annular minima of long durations, namely AR Cassiopeiae and α Coronae borealis. Their treatment can also be regarded as an illustrative example of procedures developed in preceding sections of this paper.

III. Application to AR Cassiopeiae and α Coronae borealis

6.—The eclipsing systems AR Cassiopeiae and α Coronae borealis (Gemma) have several features in common. Both consist of components that are very unequal in size and revolve around the common center of gravity in strongly eccentric orbits which are so nearly parallel to the line of sight that, at the times of conjunction, total and annular eclipses alternate. Spectrographic observations reveal that in both systems the bright component is the larger of the two, so that their primary minima are annular. In either system the secondaries are spectroscopically invisible; and both components are so far apart that their mutual distortions can be neglected even at the time of periastron passage. The range of the true anomaly during eclipses is then so small that the asymmetry of light curve arising from orbital eccentricity can be ignored; and last but not least, accurate photoelectric light curves of both these variables have been secured with the aid of a potassium cell by Stebbins,[13] who also derived excellent preliminary orbits.

7.—The light curve of AR Cassiopeiae is found to exhibit two shallow but unequally deep minima with constant phases and of slightly different durations. The fractional light intensities λ during the constant phases are, according to Stebbins,

$$\lambda_1 = 0.886 \pm 0.001 \quad \text{and} \quad \lambda_2 = 0.971 \pm 0.001,$$

respectively. Since during the constant phase of the secondary minimum (total eclipse) we observe the light of the large star alone, the fractional luminosities of both components follow at once

$$L_1 = 0.971 \pm 0.001 \quad \text{and} \quad L_2 = 0.029 \pm 0.001.$$

[12] Wyse and Kron, *Lick Observ. Bull.* 496, 1939; Kron, *Lick Observ. Bull.* 499, 1939.

[13] *Astrophys. Jour.* **54**: 81, 1921 (AR Cas); *Washburn Publ.* **15**: 41, 1928 (α CrB).

During annular phase of the primary minimum, little or no variation of light is apparent; hence, as was already pointed out by Stebbins, the darkening at limb of the large star of spectral class B3 must be small—if any. If we put, as a first approximation, $u = 0$, then for the square of the ratio of radii we have

$$k^2 = (r_2/r_1)^2 = (1 - \lambda_1)/\lambda_2, \qquad (24)$$

which yields $k = 0.346 \pm 0.004$. The remaining photometric elements as derived by Stebbins under the assumption of uniform disks are

$$r_1 = 0.192, \qquad r_2 = 0.0664, \qquad \cot i = 0.0965.$$

These are the true "elliptical" elements, with the semi-major axis of the relative orbit taken as the unit of length. Such elements do not, however, follow directly from straightforward solution of a light curve. If the orbit is eccentric, the elements directly obtained are fictitious "circular" ones, expressed in terms of the radius-vector at the moment of conjunction taken as unit. It is these elements which are to be adjusted by least squares by methods of the preceding sections. A relation between the "circular" and "elliptical" elements depends upon the eccentricity and orientation of the orbit. With the use of Stebbins' values for the orbital eccentricity $e = 0.25$ and the longitude of periastron $\omega = 37°.25$, a transition from true to fictitious (primed) elements can be made with the aid of closely approximate formulae recently derived by Sterne,[14] and the latter come out as follows:

$$r_1' = 0.161, \qquad r_2' = 0.0557, \qquad \cot i' = 0.0660.$$

Before performing the actual solution, we observe that, in the present case, the procedure described in preceding sections admits of some simplifications. First, the phase of totality during secondary minimum of AR Cassiopeiae is so long and so well observed that the accuracy with which L_1 follows directly from λ_2 is likely to exceed considerably the accuracy with which other elements can be obtained. The same applies to the ratio of radii k as obtained from equation (24). In such cases it is preferable to assume that L_1 and k are known exactly, which eliminates ΔL_1 and Δr_2 from the least-squares solution. Furthermore, the coefficients of Δu in the equations of condition of the form (4) during partial phases of the primary minimum come out on the average 10 to 50 times as small as coefficients of Δr_1 or Δi. On the other hand, during annular eclipse of the uniformly bright B3-star the coefficients of Δr_1 or Δi vanish and Δu remains the only unknown. In such a case the observations during partial phases can be employed with advantage for evaluating Δr_1 and Δi—irrespective of Δu, which can be regarded negligible on account of its small coefficient—and, with the aid of the improved elements, the assumption $u = 0$ can then be tested by observations within annular phase.

In order to save unnecessary work, observations from ascending and descending branches of the primary minimum will be combined into a more limited number of supernormals which will be used for actual work. The observational data relative to the partial phases are summarized in the following table 1*a*. Its successive

TABLE 1*a*

d	ψ	p	f^U	Δl	wt	$\frac{\partial \alpha^U}{\partial k}$	$\frac{\partial \alpha^U}{\partial p}$	$L_1\frac{\partial f}{\partial r_1}$	$L_1\frac{\partial f}{\partial i}$
0^d.0920	5°.460	−0.81	0.1128	−0.002	3	−0.035	−0.438	−0.436	+0.0602
0.1115	6.617	−0.51	0.0937	−0.001	2	−0.092	−0.595	+0.135	+0.0817
0.1200	7.121	−0.37	0.0834	−0.002	1	−0.106	−0.624	+0.323	+0.0857
0.1290	7.655	−0.23	0.0728	0.000	1	−0.112	−0.636	+0.476	+0.0873
0.1385	8.219	−0.07	0.0607	+0.006	2	−0.115	−0.633	+0.618	+0.0869
0.1525	9.050	+0.17	0.0429	+0.001	2	−0.094	−0.600	+0.759	+0.0824
0.1715	10.177	+0.49	0.0214	+0.001	2	−0.056	−0.508	+0.815	+0.0697
0.1830	10.860	+0.69	0.0104	−0.004	2	−0.029	−0.411	+0.739	+0.0564
0.2005	11.898	+0.99	0.0001	−0.011	2	0.000	−0.073	+0.151	+0.0100

TABLE 1*b*

d	ψ	p	Δl	wt	$\frac{\partial f}{\partial u}$
0^d.0050	0°.297	−1.70	−0.003	2	+0.0246
0.0175	1.039	−1.66	+0.005	2	+0.0236
0.0295	1.751	−1.58	+0.001	2	+0.0219
0.0395	2.344	−1.49	0.000	2	+0.0198
0.0470	2.789	−1.41	−0.001	1	+0.0177
0.0540	3.205	−1.34	−0.001	2	+0.0156
0.0705	4.184	−1.12	−0.002	½	+0.0081
0.0790	4.688	−1.01	0.000	½	+0.0031

columns indicate: (1), the interval (in days) from mid-primary minimum; (2), the corresponding phase-angle ψ; (3), the geometrical depth p of the eclipse as derived from Stebbins' "circular" elements; (4), the uniform loss of light $f^U = k^2\alpha^U$; (5), the residuals Δl; and (6), the weight of the respective supernormal, proportional to the number of observations included. Columns (7) and (8) then give the partial derivatives of α^U with respect to k and p at the corresponding moments, as extracted from Zessewitsch's tables.[6]

This procedure may perhaps be illustrated on the following example, in which the first entry of column (8) is to be evaluated. Interpolating

[14] *Proc. Nat. Acad. Sci.* **26**: 36, 1940.

in Zessewitsch's table,[15] we find that, for $k = 0.346$,

p	α^U	Δ'	Δ''	Δ'''
−0.79	0.93322			
		+451		
−0.80	0.93773		−9	
		+442		0
−0.81	0.94215		−9	
		+433		−1
−0.82	0.94648		−10	
		+423		
−0.83	0.95071			

Now from the calculus of finite differences (by differentiation of Stirling's formula), it follows that

$$h\frac{\partial\alpha}{\partial p} = \frac{1}{2}(\Delta'_{-\frac{1}{2}} + \Delta'_{\frac{1}{2}}) - \frac{1}{12}(\Delta'''_{-\frac{1}{2}} + \Delta'''_{\frac{1}{2}}) + \cdots, \quad (25)$$

where the Δ's stand for the respective adjacent differences and h is the interval of tabulation. In our present case $h = -0.01$ and, if we propose to evaluate the derivative at $p = -0.81$, $\Delta'_{-\frac{1}{2}} = 0.00442$ and $\Delta'_{\frac{1}{2}} = 0.00433$. The third differences oscillate in sign and can therefore be neglected. Equation (25) then gives -0.438 for the value of the derivative, correct to three significant figures, which is an ample accuracy for our purpose. An alternative computation of the derivative by means of a (central) 5-point formula

$$h\frac{\partial\alpha}{\partial p} = \frac{1}{12}\{\alpha_{-2} - 8\alpha_{-1} + 8\alpha_1 - \alpha_2\} \quad (26)$$

leads to exactly the same result.

The final columns (9) and (10) of table 1*a* give the coefficients of Δr_1 and Δi in the equations of condition of the form (4) as computed with the aid of equations (14). As many decimals are retained as are regarded to be reliable. The normal equations for Δr_1 and Δi then take the forms

$$\begin{aligned} 2.73920\Delta r_1 + 0.26945\Delta i + 0.000776 &= 0, \\ + 0.04772\Delta i - 0.000034 &= 0, \end{aligned}$$

and their solution yields

$$\begin{aligned} \Delta r_1 &= -0.0008 \pm 0.0014 \text{ (p.e.)}, \\ \Delta i &= +0.0017 \pm 0.0033 \\ &= +0°.3 \pm 0°.6 \quad \text{(p.e.)}. \end{aligned}$$

[15] *Bull. Inst. Astron. Leningrad* 50: table V, 1940.

Both corrections come out insignificant. Stebbins' circular elements are thus found as good as they can possibly be.

It remains for us to investigate the extent to which our initial assumption $u = 0$ for the principal component of AR Cassiopeiae can be considered legitimate. This can be ensured by an analysis of Stebbins' observations during annular phase of the primary minimum. Under an assumption of uniform disks, equations (4) reduce to

$$\Delta l = -L_1\frac{\partial f}{\partial u}\Delta u,$$

and each normal observed within annular phase leads then to an independent determination of Δu. The following table 1*b* again summarizes the relevant observational data. The headings of the individual columns are now self-explanatory. The uniform loss of light during annular eclipse of a uniformly bright disk is naturally constant and equal to k^2. A weighted mean from 8 supernormals listed in table 1*b* is

$$\Delta u = 0.003 \pm 0.031 \text{ (p.e.)}.$$

The errors of k and p (*i.e.*, of i) combined make the $\partial f/\partial u$'s uncertain on the average by about 25 percent, which means that the true error of Δu is probably closer to 0.04. But in the light of the above analysis it appears probable that the darkening at limb of the B3-component of AR Cassiopeiae at λ 4500 A—if any—does not exceed 0.04.

8.—The eclipsing system of α Coronae borealis (Gemma) presents but a slightly different case. Spectroscopic observations prove again the bright component to be the larger of the two; but in contrast to AR Cassiopeiae the light curve of Gemma shows only one observable eclipse. Stebbins' measures have ruled out the possibility of a secondary minimum deeper than 0.01 magn. at any point of the light curve. Since, according to Stebbins, $\lambda_1 = 0.908$ while $1 - \lambda_2 > 0.009$, the ratio of mean surface brightnesses J_2/J_1 of the two components must be smaller than one-tenth. This, coupled with Stebbins' ratio of radii $k = 0.28$ derived from the light curve shows that

$$L_1 \geqslant 0.992 \quad \text{while} \quad L_2 \leqslant 0.008.$$

In the absence of an observable secondary minimum, little can be done in the way of obtaining a more precise value of J_2/J_1 and so of the fractional luminosities. It is also apparent,

however, that an approximation $L_1 = 1$ involves very little risk and will introduce little uncertainty in subsequent computations. The light changes within annular phase of the primary minimum being continuous, the darkening of the large star cannot be neglected. Stebbins solved for the photometric elements of Gemma by Russell's method, assuming central eclipse ($i = 90°$), and got the following results:

$$r_1 = 0.0671, \qquad r_2 = 0.0189, \qquad u = 0.5.$$

These are the "circular" elements which we are going to adjust by the method of least squares.

Before performing the solution, we find it again convenient to group Stebbins' observations from the ascending and descending branches of the primary minimum into 11 supernormals which are given in the following table 2. The

TABLE 2

d	ψ	p	f	Δl	wl	$\frac{\partial f}{\partial r_1}$	$\frac{\partial f}{\partial r_2}$	$\frac{\partial f}{\partial u}$
0^d.015	0°.31	−3.26	0.0967	−0.001	12	−3.492	+12.43	+0.0328
0.026	0.54	−3.05	0.0961	+0.005	12	−3.369	+12.03	+0.0322
0.040	0.83	−2.78	0.0956	+0.001	12	−3.229	+11.60	+0.0313
0.066	1.37	−2.29	0.0933	−0.003	23	−2.886	+10.63	+0.0270
0.094	1.95	−1.75	0.0890	+0.004	22	−2.419	+9.598	+0.0189
0.122	2.52	−1.22	0.0821	−0.002	24	−1.829	+8.501	+0.0058
0.151	3.13	−0.66	0.0639	−0.013	9	+0.533	+5.589	−0.0096
0.168	3.48	−0.34	0.0477	−0.011	5	+0.830	+4.460	−0.0123
0.177	3.67	−0.16	0.0385	−0.004	8	+0.915	+3.904	−0.0125
0.191	3.96	+0.10	0.0261	+0.002	3	+0.874	+3.143	−0.0115
0.203	4.21	+0.33	0.0164	+0.009	9	+0.686	+2.487	−0.0093

headings of its columns require no further explanation. The weight of each supernormal is put equal to the number of sets of observations included. The observations during partial and annular phase of primary minimum are now treated simultaneously. Since the preliminary value of $i = 90°$, $\partial f/\partial i = 0$. This naturally leaves Δi indeterminate; but at the same time makes other corrections nearly independent of it. Eleven equations of condition for Δr_1, Δr_2, and Δu are formed by the method of section II; the normal equations become

$$\begin{aligned} 825.88\Delta r_1 - \ 2948.4\Delta r_2 - \ 7.2161 \ \Delta u &= +\ 0.20127, \\ +\ 12151.6\Delta r_2 + 24.2008 \ \Delta u &= +\ 0.38893, \\ +\ 0.066527\Delta u &= -\ 0.0028101, \end{aligned}$$

and their solution yields

$$\begin{aligned} \Delta r_1 &= 0.0027 \pm 0.0031 \text{ (p.e.)}, \\ \Delta r_2 &= 0.0007 \pm 0.0003 \text{ (p.e.)}, \\ \Delta u &= 0.01 \ \pm 0.24 \ \text{ (p.e.)}. \end{aligned}$$

Only the correction for Δr_2 is probably significant; and, in consequence, $k = 0.281 \pm 0.047$ (p.e.).

9.—The definitive circular elements of AR Cassiopeiae and α Coronae borealis together with their probable errors are collected in the following tabulation:

		AR Cassiopeiae	Gemma
Orbital period	P	6^d.0663	17^d.360
Duration of the primary minimum	D	0^d.401±0^d.014	0^d.492±0^d.009
Duration of the annular phase	d	0^d.158±0^d.010	0^d.280±0^d.007
Fractional light of the large star	L_1	0.971±0.001	$\geqslant$ 0.992
Fractional light of the small star	L_2	0.029±0.001	$\leqslant$ 0.008
Radius of the large star	r_1	0.1602±0.0014	0.0698±0.0031
Radius of the small star	r_2	0.0554±0.0005	0.0196±0.0003
Ratio of radii	k	0.346±0.004	0.281±0.047
Orbital inclination	i	86°.5±0°.6	90° (assumed)
Degree of limb-darkening at 4500 A	u	0.00±0.04	0.51±0.24

The conversion of the fictitious circular elements into true elliptical ones would presume a discussion of relevant spectroscopic data (moving apsides), which is beyond the scope of the present paper.

A marked difference in limb-darkenings of bright components in these two systems was already commented upon by Stebbins.[13] It is interesting, in this connection, to compare the darkenings at $\lambda = 4500$ A of the following three stars:

Star	*Spectrum*	u	*Authority*
AR Cas A	B3	0.00±0.04	Present investigation
YZ Cas A	A3	0.49±0.04	Kron, *Lick Observ. Bull.* 499, 1939
Sun	G0	0.74±0.02	Abbot, Fowle, and Aldrich, *Ann. Astron. Observ. Smithsonian Inst.* **4**: 221, 1922

A decrease of u with increasing effective temperature is clearly indicated. A comparison with the theory shows that the hypothesis of a constant coefficient of continuous absorption in stellar atmospheres is plainly at variance with darkening as small as was found for AR Cas A. If variation of the absorption coefficient with the temperature is taken into account, the comparison becomes more favorable; but we meet a similar discrepancy as was noted for color temperatures of the stars: namely, that the observed coefficients of darkening correspond to those computed theoretically for temperatures by about 3000° higher than those usually accepted for the respective spectral class.

THE EFFECTS OF REFLECTION UPON LIGHT AND VELOCITY CURVES OF CLOSE BINARY SYSTEMS

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ABSTRACT

In the first part of the present paper the amount of total light reflected by components of eclipsing binary systems out of eclipses as well as within minima is investigated to the degree of accuracy to which the components can be regarded as spheres. The variation of reflected light between minima is found to mask the ellipticity effect in close binaries to a greater extent than has been generally realized; while within minima a light curve representing the loss of reflected light would closely resemble one due to the eclipse of a disk which is completely darkened at limb. Simple formulae are further given for the reduction of heat curves into light curves observed in more or less narrow spectral ranges, which should enable us to compare the theoretical results with observations. Finally it is pointed out how the phase-law becomes modified if the components of a binary describe eccentric orbits.

The second part contains an analysis of the effects of reflection upon velocity curves of spectroscopic binary systems. The reflected light, like the darkening of distorted stars, allows the axial rotation of the components to contribute to their observed radial velocities. The contribution of reflection is found systematically to diminish the amplitudes of the orbital velocity curves and to make their ascending branches steeper than the descending ones. The former part will cause all mass-functions and masses of the stars derived from velocity curves uncorrected for reflection to be underestimated; the latter will simulate an eccentric orbit with the longitude of periastron at 270°. In close binaries the spurious eccentricity arising from reflection will tend to reinforce that due to limb-darkening, and neutralize that due to gravity-darkening, of tidally distorted components. The eccentricity-simulating effects of both ellipticity and reflection are found quantitatively inadequate to account for the observed clustering of the longitudes of periastra of spectroscopic binaries in the neighborhood of 90°.

1.—IT is inevitable in close binary systems that a part of radiation of either component sent out in every direction will fall on the surface of its mate where it will be absorbed and re-emitted (or possibly scattered). This effect will evidently cause the hemispheres exposed to the incident radiation to be brighter than those turned away; and as the components revolve, the amount of light reflected[1] in any direction inclined to the orbital plane will vary with the phase. The resulting changes of light are indeed conspicuous in light curves of several known binaries and had been detected long ago.[2] Variations of a similar nature should, moreover, manifest themselves also in the velocity curves of spectroscopic binary systems. The photometric implications of the reflection effect have already been the subject of several investigations by various writers, and the variation of total light reflected out of eclipses is at present satisfactorily understood, at least to a first approximation. On the other hand, little or no systematic work has so far been done in the way of investigating the effects of reflected light upon the star's radial velocity.

The present paper will consist essentially of two parts. In the first one (sections 2–7) we propose to investigate the total amount of reflected light and its variation out of eclipses as well as within minima. In doing so we shall drop the conventional assumption that the incident and reflected light form parallel beams. We shall take into account the convergence of the incident beam to the degree of accuracy to which the reflecting component can be regarded as a sphere. Formulae will further be given for the reduction of bolometric curves into light curves observed in more or less narrow spectral ranges (visual, photographic, etc.), which should enable us to compare the theoretical formulae with observations. It will also be pointed out how the phase-law becomes modified if the components of a binary revolve in eccentric orbits. In the second part (sections 8–10) of this paper the effects of reflection upon velocity curves of spectroscopic binary systems will be investigated. It will be shown how the light reflected from rotating components contributes to their radial velocities and how this contribution, when not allowed for, would systematically

[1] This term will hereafter be used for convenience and in technical sense only; for the actual process is absorption followed by re-emission.

[2] *Cf.* Dugan, *Science* **28**: 854, 1908; Stebbins, *Astrophys. Jour.* **32**: 213, 1910; Nordmann, *Bull. astron.* **27**: 145, 1910.

vitiate certain elements of their spectroscopic orbits.

I. Photometric Effects

2.—In order to be able to evaluate the effects of reflection upon light of close binary systems, it is prerequisite to ascertain the albedo of their components. The answer to this problem has been supplied by Eddington[3] and Milne,[4] who proved that if a star is to be in radiative equilibrium, all radiation incident upon it from outside must be wholly re-radiated—or, in other words, its heat-albedo must be unity. The incident radiation will exert an additional pressure on the boundary of the reflecting star. It will re-arrange the temperature-distribution in the atmosphere over the illuminated hemisphere; in particular, it will increase its surface temperature out of proportion to its effective temperature as judged by the increase in surface brightness. But all these effects are too small to influence the interior of the reflecting star to any appreciable extent, and its equilibrium remains unchanged.

For the moment we pass over the problem of translating a heat curve into a light curve observed in a limited spectral range and confine our attention to the amount of energy reflected. This problem is essentially a geometrical one and can be dealt with as follows. Let us adopt a rectangular frame of reference, with origin at the center of gravity of the reflecting star which we shall refer to as the primary component, chosen so that the Z-axis is constantly in the direction of the secondary (illuminating) component while the Y-axis is perpendicular to the orbital plane. The direction cosines λ, μ, ν of any radius-vector in this system clearly are

$$\lambda = \cos\phi \sin\theta,$$
$$\mu = \sin\phi \sin\theta,$$
$$\nu = \cos\theta,$$

where θ, ϕ denote the polar distance and longitude, measured from the Z-axis, of any surface point of the primary star. As the components revolve, this system of axes evidently rotates with respect to the line of sight; and if i denotes the inclination of the orbital plane to the celestial sphere and ψ the longitude of the secondary component measured from inferior conjunction, the direction cosines l_0, m_0, n_0 of the line of sight become

$$l_0 = \cos\psi \sin i,$$
$$m_0 = \sin\psi \sin i,$$
$$n_0 = \cos i.$$

The amount of light L_1^* re-radiated by the primary component in the direction of the line of sight then takes the form

$$L_1^*(\psi, i) = \int_0^{\pi} \int_{\epsilon-\pi/2}^{\pi/2} r^2 I \cos\gamma \sin\theta d\theta d\phi, \quad (1.0)$$

where r specifies the boundary of the reflecting star; I, the intensity-distribution of the reflected radiation; γ, the angle of foreshortening; and ϵ, that between the Z-axis and the line of sight. Evidently

$$\cos\epsilon = l_0 = \cos\psi \sin i,$$

while

$$\cos\gamma = ll_0 + mm_0 + nn_0,$$

where l, m, n are direction cosines of a line normal to the surface r.

Let R denote the separation of centers of the two components. Since the intensity of incident radiation is inversely proportional to R^2, the amount of reflected light (which is proportional to the exposed area) will evidently be a quantity of the order of $(r/R)^2$. The boundary r is, strictly speaking, not independent of direction; for the primary component must suffer distortion owing to its own rotation and the tidal action of its companion. The theory shows that the distortion becomes manifest in quantities of the order of $(r/R)^3$; hence the amount of reflected light would be affected by distortion in terms of the order of $(r/R)^5$. In order to avoid far-reaching complications, we propose hereafter to work consistently up to quantities of the order of $(r/R)^4$—*i. e.*, to the degree of accuracy to which the components can be regarded as spheres and r as a constant which we denote r_1. If so, then

$$l = \lambda, \qquad m = \mu, \qquad n = \nu,$$

and $\cos\gamma$ becomes specified.

3.—The distribution of the reflected radiation has been investigated in detail by Milne.[4] He found that if a beam of flux πS per unit cross-section is incident at angle α to an arbitrary point P (*cf.* fig. 1) on the boundary of a star in radiative equilibrium, the radiation emerges as a diffuse beam whose intensity I in the direction

[3] *Royal Astron. Soc. Monthly Notices* **86**: 320, 1926.
[4] *Royal Astron. Soc. Monthly Notices* **87**: 43, 1927.

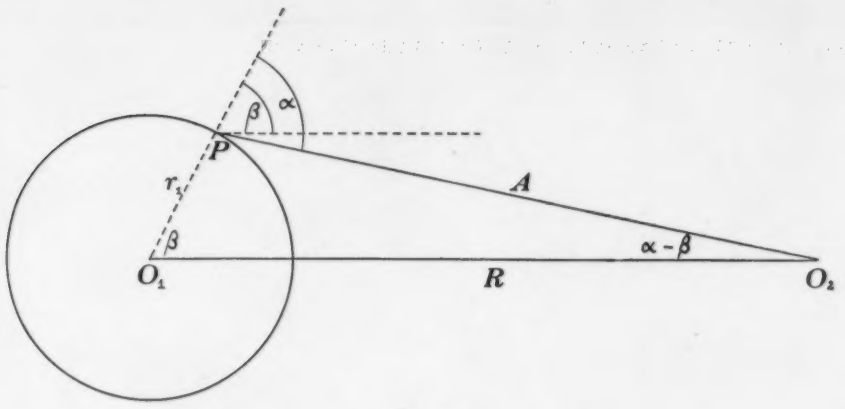

FIG. 1.

of the line of sight becomes

$$I = S \cos \alpha \left\{ \frac{(\cos \alpha + \tfrac{1}{2})(\cos \beta + \tfrac{1}{2})}{\cos \alpha + \cos \beta} \right\}, \quad (2.0)$$

where the angles α and β of incidence and reflection (*cf.* fig. 1) are clearly related by

$$\sin (\alpha - \beta) = (r_1/R) \sin \alpha. \quad (3)$$

The law (2.0) is not exact, but is supposed to be a close approximation. Its form is, moreover, complex; and its introduction in (1.0) would lead to considerable analytic difficulties. It is, therefore, proper to enquire whether or not (2.0) could without appreciable loss of accuracy be replaced by some other law of simpler form which would be easier to deal with. If r_1/R is very small, then β is sensibly equal to α and (2.0) reduces to

$$I = \tfrac{1}{2}S(\cos \alpha + \tfrac{1}{2})^2; \quad (2.1)$$

but then the reflection itself is very small and should be hardly noticeable. It may be pointed out, however, that when the components get closer and $\alpha \neq \beta$, the expression in curly brackets on the right-hand side of (2.0) varies but very little from center to limb and is, on the average, slightly larger than unity. Numerical computations reveal indeed that for all reasonable values of r_1/R a simplified law

$$I = \frac{17}{16} S \cos \alpha \quad (2.2)$$

offers a practically equivalent approximation.

The relative accuracy of the formulae (2.0) and (2.2) is graphically illustrated on figure 2, where their respective errors (expressed in terms of incident light) are plotted against $\cos \alpha$. The dots and dashes represent the deviations from reality of the complex formula (2.0) according to data published by Milne,[5] while the dashed lines give residuals left by (2.2) for five values of r_1/R ranging from 0.10 to 0.30. The plot shows Milne's complete formula to be accurate within 4 percent of the incident flux. In a narrow annulus near the limb the simplified equation (2.2) may depart more from reality if r_1/R is small; but then the reflection itself is small; and with increasing r_1/R the fit steadily improves until for r_1/R approximately one-third equations (2.0) and (2.2) become again practically equivalent. It is therefore obvious that over most of the disk no appreciable gain in accuracy could be expected if Milne's complete formula (2.0) were preferred to the simpler equation (2.2); and in what follows the latter will be adopted. Its form is analogous to (though not identical with) Lambert's cosine law. Within the scheme of our approximation we consider the intensity of the reflected radiation to vary as the cosine of the angle of incidence, while Lambert's law involves the angle of foreshortening; and these two are not identical for any finite value of r_1/R.

The flux of radiation incident at any surface point of the primary component becomes

$$\pi S = \frac{\mathfrak{L}_2}{4\pi A^2}, \quad (4)$$

where A denotes that point's distance from the secondary, and $\mathfrak{L}_2$ stands for the secondary's total energy output. From the triangle O_1O_2P

[5] *Op. cit.*, p. 48.

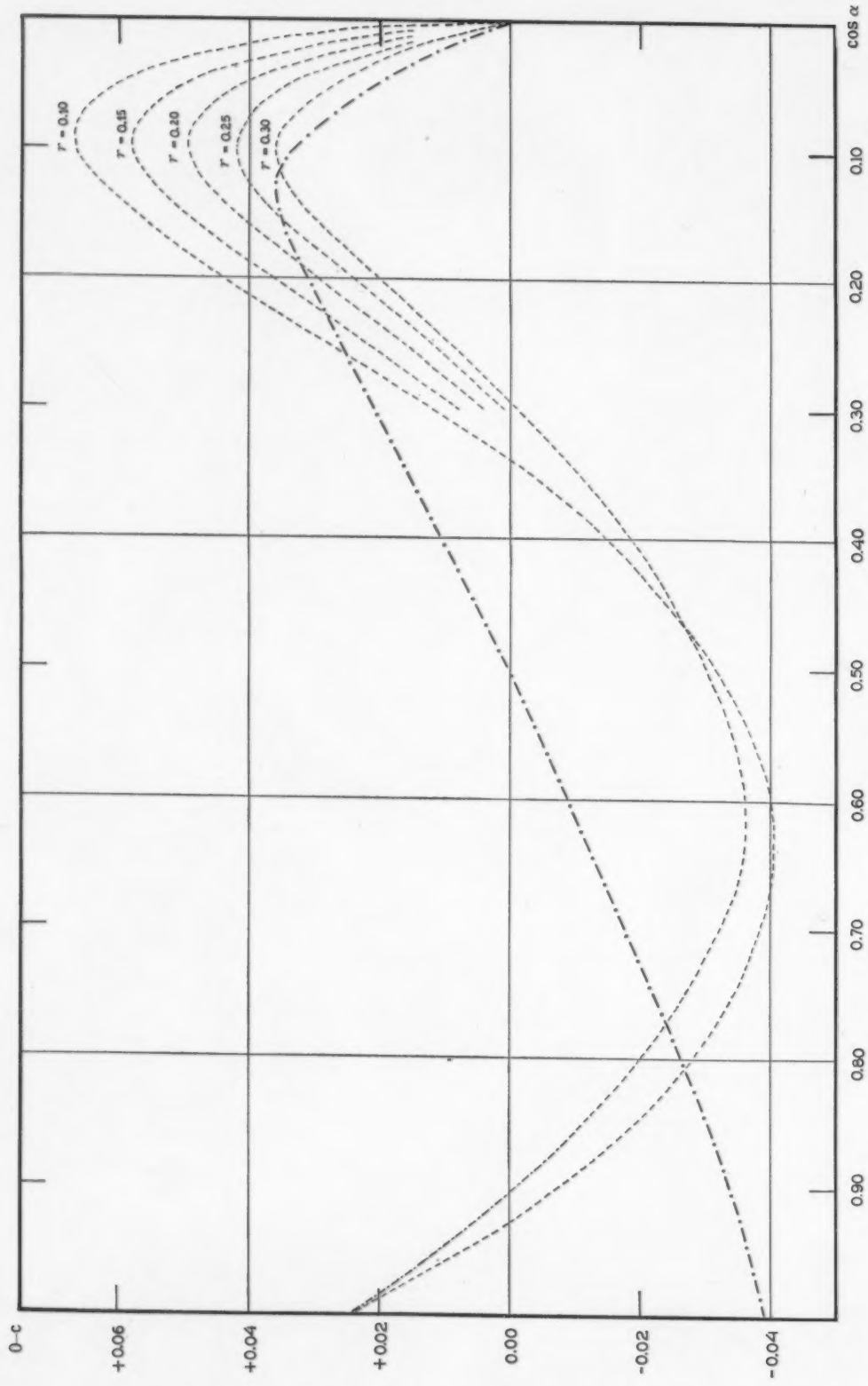
r = 0.10
r = 0.15
r = 0.20
r = 0.25
r = 0.30
cos α
0.10
0.20
0.30
0.40
0.50
0.60
0.70
0.80
0.90
O–C
+0.06
+0.04
+0.02
0.00
-0.02
-0.04

FIG. 2.

(fig. 1) we have

$$A = R\sqrt{1 - 2\left(\frac{r_1}{R}\right)\cos\beta + \left(\frac{r_1}{R}\right)^2}, \quad (5)$$

and

$$\cos\alpha = \frac{\cos\beta - r_1/R}{\sqrt{1 - 2\left(\frac{r_1}{R}\right)\cos\beta + \left(\frac{r_1}{R}\right)^2}}. \quad (6)$$

Furthermore,

$$\frac{1}{\sqrt{1 - 2\left(\frac{r_1}{R}\right)\cos\beta + \left(\frac{r_1}{R}\right)^2}} = \sum_{j=0}^{\infty}\left(\frac{r_1}{R}\right)^j P_j(\cos\beta),$$

where the P_j's are Legendre polynomials of various orders and β, the angle of foreshortening along the Z-axis, is evidently equal to $\cos^{-1}\lambda$. If we now combine equations (2.2) and (4)–(6) the integrand of (1.0) takes the neat form

$$\pi r_1^2 I = \frac{17}{16}\left\{\left(\frac{r_1}{R}\right)^2 P_1(\lambda) + 2\left(\frac{r_1}{R}\right)^3 P_2(\lambda) + 3\left(\frac{r_1}{R}\right)^4 P_3(\lambda) + \cdots\right\} L_2, \quad (7)$$

where the total energy output of the secondary component $\mathfrak{L}_2$ was replaced by its observed luminosity $L_2 = \mathfrak{L}_2/4\pi$.

4.—Equation (1.0) could now be solved as it stands. Before performing the integration, however, we find it advantageous to change over to another rotating system of coordinates $X'Y'Z'$ having the same origin, but whose Z'-axis is constantly coincident with the line of sight while the X'-axis is in the direction of projected center of the secondary component. Let x, y, z be the direction cosines of any radius-vector in the primed system. Then

$$\lambda = x\sin\epsilon + z\cos\epsilon,$$

where, evidently, $z^2 = 1 - x^2 - y^2$ and $\sin\epsilon = \sqrt{1 - l_0^2}$. The direction cosines x and y can be regarded as rectangular coordinates in a plane $z = 0$ which is tangent to the celestial sphere. Let us therefore adopt x and y as the new independent variables. The surface element $\cos\gamma\sin\theta d\theta d\phi$ then reduces merely to $dxdy$ and equation (1.0) takes the form

$$L_1^*(\psi, i) = \left\{\int_{-1}^{+1}\int_{0}^{\sqrt{1-y^2}} - \int_{-1}^{+1}\int_{0}^{l_0\sqrt{1-y^2}}\right\} r_1^2 I\, dxdy. \quad (1.1)$$

Its integration yields

$$\pi L_1^*(\psi, i) = \frac{17}{16}\left\{\frac{2}{3}\left(\frac{r_1}{R}\right)^2[(\pi - \epsilon)\cos\epsilon + \sin\epsilon] + \frac{\pi}{8}\left(\frac{r_1}{R}\right)^3[3\cos^2\epsilon + 2\cos\epsilon - 1] - \left(\frac{r_1}{R}\right)^4\sin^3\epsilon + \cdots\right\} L_2, \quad (8.0)$$

where $\cos\epsilon = \cos\psi\sin i$. This is the law expressing the amount of total reflected light and its variation with the phase. If we retain only the first term of the order of $(r_1/R)^2$ (*i. e.*, consider the beams of incident and reflected light as parallel), the result is one derived long ago in connection with planetary phases. If, however, the two bodies approach closer (as in binary systems), this approximation becomes obviously inadequate, and terms of higher orders must be taken into account.

Equation (8.0) expanded in terms of Legendre polynomials becomes

$$\begin{aligned}\frac{16}{17}\frac{L_1^*}{L_2} = &\left\{\frac{1}{4}\left(\frac{r_1}{R}\right)^2 - \frac{3}{16}\left(\frac{r_1}{R}\right)^4 + \cdots\right\} P_0(l_0)\\ &- \left\{\frac{1}{3}\left(\frac{r_1}{R}\right)^2 + \frac{1}{4}\left(\frac{r_1}{R}\right)^2 + \cdots\right\} P_1(l_0)\\ &+ \left\{\frac{5}{64}\left(\frac{r_1}{R}\right)^2 + \frac{1}{4}\left(\frac{r_1}{R}\right)^3 + \frac{15}{64}\left(\frac{r_1}{R}\right)^4 + \cdots\right\} P_2(l_0)\\ &+ \left\{\frac{1}{256}\left(\frac{r_1}{R}\right)^2 - \frac{81}{2048}\left(\frac{r_1}{R}\right)^4 + \cdots\right\} P_4(l_0) + \cdots.\end{aligned} \quad (8.1)$$

If we leave the constant terms aside, in the absence of eclipses $(16/17)(L_1^*/L_2)$ is found to vary as

$$\begin{aligned} &-\left\{\frac{1}{3}\left(\frac{r_1}{R}\right)^2 + \frac{1}{4}\left(\frac{r_1}{R}\right)^3 + \cdots\right\}\cos\epsilon \\ &+\left\{\frac{16}{27\pi^2}\left(\frac{r_1}{R}\right)^2 + \frac{3}{16}\left(\frac{r_1}{R}\right)^3 + \frac{8}{5\pi^2}\left(\frac{r_1}{R}\right)^4 + \cdots\right\}\cos 2\epsilon \\ &+\left\{\frac{16}{675\pi^2}\left(\frac{r_1}{R}\right)^2 - \frac{8}{35\pi^2}\left(\frac{r_1}{R}\right)^4 + \cdots\right\}\cos 4\epsilon + \cdots \end{aligned} \tag{8.2}$$

or

$$\begin{aligned} &-\left\{\frac{1}{3}\left(\frac{r_1}{R}\right)^2 + \frac{1}{4}\left(\frac{r_1}{R}\right)^3 + \cdots\right\}\cos\epsilon \\ &+\left\{\frac{1}{3\pi}\left(\frac{r_1}{R}\right)^2 + \frac{3}{8}\left(\frac{r_1}{R}\right)^3 + \frac{3}{2\pi}\left(\frac{r_1}{R}\right)^4 + \cdots\right\}\cos^2\epsilon \\ &+\left\{\frac{1}{36\pi}\left(\frac{r_1}{R}\right)^2 - \frac{3}{8\pi}\left(\frac{r_1}{R}\right)^4 + \cdots\right\}\cos^4\epsilon + \cdots. \end{aligned} \tag{8.3}$$

We thus find that to the order of accuracy we are working, the solution of (1.0) or (1.1) can be developed in a series of even-order harmonics in cos ϵ—plus a single odd harmonic of order one—with power series in r_1/R as coefficients. These series, unfortunately, do not converge very rapidly with increasing power of r_1/R; and their convergence becomes the slower, the higher the order of the respective harmonic.[6] Unless r_1/R is small, the first few terms given in equations (8.1)–(8.3) may indeed not specify the coefficients of higher harmonics with sufficient precision. This is an unpleasant fact; for in light curves of real binary systems these terms will superpose upon variations of similar order of magnitude invoked by the ellipticity of the components; and unless the effects of reflection can be predicted by the theory, the ellipticity proper cannot be satisfactorily isolated from observations.

Equation (8.0) refers to the light reflected from the primary star alone. The amount of the primary's light reflected from the secondary component and its variation with the phase will also be governed by an equation of the form (8.0) if only indices are interchanged and ϵ is replaced by $\pi - \epsilon$. This difference in phase will evidently change the sign of the only odd harmonic of the first order, but not of even harmonics. It follows, therefore, that in the combined light of a binary system terms arising from reflection of light on either component and associated with the first harmonic will always tend to neutralize each other, while those associated with even harmonics will always reinforce.

5.—So far we have considered the relative orbits of the components to be circular. Eccentric orbits are exceptional among close binary systems; but since such exceptions exist, it seems appropriate to consider the way in which the foregoing results may be affected by orbital eccentricity. If the orbit happens to be eccentric, the phase-angle ψ is no longer proportional to the time but becomes identical (except for the origin) with the true anomaly v in the relative orbit. Further, r_1/R is no longer constant, but equal to

$$(r_1/p)(1 + e\cos v),$$

where e denotes the orbital eccentricity and p the semi-latus rectum of the relative orbit. The reflection effect then ceases to be symmetrical with respect to conjunctions, and the law of reflected radiation can be followed only numerically.

In order to do so, we convert first the mean anomaly into the true anomaly (which presumes a knowledge of orbital eccentricity and of the longitude of periastron) and compute the values of ψ and r_1/R for any given moment; equation (8.0) then continues to give the correct amount of reflected light. On the other hand, since the amount of reflection in eccentric binary systems varies rapidly with varying radius-vector, the form of the observed reflection effect may under favorable circumstance indicate to inspection the approximate position of the periastron. For an

[6] The existence of a term of the order of $(r_1/R)^2$ in the coefficient of cos 2ϵ in (8.2) was already pointed out by Eddington (*Royal Astron. Soc. Monthly Notices* **86**: 320, 1926); but it appears presently that unless r_1/R is very small, this term alone will not specify the true magnitude of the coefficient of cos 2ϵ.

illustrative example of such a situation the reader is referred to a study of the reflection effect in the system of ζ Aurigae (where $e = 0.43$) by Walter.[7]

6.—Equation (8.0) governing the variation of reflected light with the phase is valid irrespective of whether or not a binary system is an eclipsing variable. The variation evidently ceases only if the line of sight happens to be perpendicular to the orbital plane; for then $\epsilon = 90°$ regardless of ψ, and the reflected radiation contributes a constant amount to the proper light of a system. With increasing inclination the phase-effect becomes progressively more pronounced until it reaches a maximum at $i = 90°$. If, however, i is anywhere near 90°, it is probable that at the time of conjunctions eclipses will occur. During eclipse a system suffers then a loss of the proper light of the eclipsed star plus light reflected upon it; for the portion of either component which can undergo eclipse is necessarily illuminated.

Let us, in what follows, investigate the form of a light curve that would result from the loss of light reflected by the star undergoing eclipse. The respective loss of reflected light $\Delta\mathfrak{L}$ can be found by integrating

$$r^2 I \cos\gamma \sin\theta d\theta d\phi$$

within limits extending over the whole visible portion. This integral becomes again tractable in terms of the xy-coordinates introduced in section 4, and during partial eclipse* it takes the form

$$\left\{ \int_s^1 \int_{-\sqrt{1-x^2}}^{+\sqrt{1-x^2}} + \int_{\delta-k}^{s} \int_{-\sqrt{k^2-(\delta-x)^2}}^{+\sqrt{k^2-(\delta-x)^2}} \right\} I r_1^2 dxdy, \quad (9)$$

where $k = (r_2/r_1)$, $\delta = (R/r_1)\sin\epsilon$, and

$$s = \frac{r_1^2 - r_2^2 + \delta^2}{2\delta r_1}.$$

In the neighborhood of conjunctions $\cos\epsilon$ approaches unity and $\sin\epsilon$ therefore goes to zero. If the squares and higher powers of $\sin\epsilon$ are neglected, the theoretical light curve within eclipses becomes independent of the scale of each particular system and we obtain

$$\Delta\mathfrak{L} = \frac{17}{16}\left(\frac{r_1}{R}\right)^2 \left\{ \alpha_1{}^0 + (3\alpha_2{}^0 - \alpha_0{}^0)\frac{r_1}{R} + \frac{3}{2}(5\alpha_3{}^0 - 3\alpha_1{}^0)\left(\frac{r_1}{R}\right)^2 + \cdots \right\} L_2, \quad (10)$$

where we have abbreviated

$$\pi\alpha_n{}^m = \left\{ \int_s^1 \int_{-\sqrt{1-x^2}}^{+\sqrt{1-x^2}} + \int_{\delta-k}^{s} \int_{-\sqrt{k-(\delta-x)^2}}^{+\sqrt{k-(\delta-x)^2}} \right\} x^m z^n dxdy. \quad (11)$$

This latter equation defining the so-called associated α-functions has recently been integrated by the writer for all values of m and n required in the theory of light curves of close binary systems, including those which occur in the present problem. For their explicit forms, which are too long to be quoted here, the reader is referred to the writer's recent memoir.[8] The associated α-functions are by definition dimensionless quantities depending on two independent variables (such as the ratio of radii of the two components and the geometrical depth of the eclipse) and can be tabulated in terms of such parameters in the way as has been done for two associated α-functions of lowest orders which express the fractional loss of light of a uniformly bright disk ($\alpha_0{}^0$) or of one completely darkened at limb ($\frac{3}{2}\alpha_1{}^0$). Associated α-functions of higher orders and indices are, unfortunately, not yet available in tabular form. Those of zero-order ($m = 0$), which alone figure in the present problem within the above scheme of approximation, increase monotonically from zero at the moment of first contact to $2/(2 + n)$ at the beginning of totality. When therefore the reflecting star gets totally eclipsed, equation (10) yields

$$\frac{17}{16}\left\{ \frac{2}{3}\left(\frac{r_1}{R}\right)^2 + \frac{1}{2}\left(\frac{r_1}{R}\right)^3 + \cdots \right\} L_2$$

in agreement with (8.0).

The reader may recall that $\frac{3}{2}\alpha_1{}^0$ expresses the loss of light of a disk which is completely darkened at limb. A glance at equation (10) shows that $\alpha_1{}^0$ is the only zero-order term on its right-hand side. It follows, therefore, that if

[7] *Zeitschr. f. Astrophys.* **14**: 62, 1937.

* If the eclipse is annular, the first double integral in (9) (and also in equation 11) vanishes, and the upper limit of integration with respect to x becomes $\delta + k$ instead of s.

[8] *Proc. Am. Philos. Soc.* **85**: 399, 1942.

the eclipsed star had no light of its own and the observed minimum were due entirely to the loss of reflected radiation, the observed light curve would closely approximate that of an eclipse of a completely darkened disk. This could indeed have been anticipated; for if r_1/R is small, the angles of incidence and reflection are sensibly equal and equation (2.2) then gives a total darkening at limb.

7.—Formulae for the variation of reflected light between eclipses as well as within minima developed thus far have all been based on the assumption that the albedo of the reflecting star is unity. The validity of this assumption is evident only for integrated light; and our equations (8.0) or (10) are therefore applicable without reserve only to radiometric light curves —provided that these could be properly corrected for atmospheric absorption. If, however, our theory is to be compared with observations carried out in limited spectral ranges, the heat curves have first to be translated into light curves relevant to a given effective wavelength. For if the illuminating and reflecting components differ in spectra, the incident light is going to be re-radiated at a different temperature (generally slightly higher than the proper temperature of the reflecting star). All incident light is to be reflected; hence the Planck curves specifying the incident and reflected radiations will subtend equal areas; but their maxima may be considerably displaced and relative intensities of both radiations at any particular wavelength may widely differ. In consequence, it is to be expected that, unless the temperatures of both components are very nearly equal, the observed efficiency of the incident and reflected radiation will be generally different.[9] The observed reflection may be either greater or smaller than that expected for total radiation, depending on temperatures of the two components.

Let us investigate this process quantitatively and confine our attention to light emitted by the secondary (illuminating) component. Its observed efficiency will evidently be

$$\frac{\mathfrak{L}_2}{4\pi}\left(\frac{J_\lambda}{J_b}\right)_2,$$

where $\mathfrak{L}_2$ stands for the secondary's total energy output and J_b, J_λ denote its surface brightnesses in total and observed light. A fraction q of total light of the secondary component gets reflected from the primary star in the direction of the line of sight. Since the heat-albedo of the primary is unity, the observed amount of reflected light will be

$$q\frac{\mathfrak{L}_2}{4\pi}\left(\frac{J_\lambda}{J_b}\right)_1.$$

The observed efficiency of the incident radiation is, however, known; for

$$\frac{\mathfrak{L}_2}{4\pi}\left(\frac{J_\lambda}{J_b}\right)_2 = L_2, \tag{12}$$

where L_2 is the fractional luminosity of the secondary which in eclipsing systems follows readily from observations. If we now eliminate $\mathfrak{L}_2$ by means of (12), we obtain that the amount of light L^* of star i reflected from star j in the direction of the line of sight and observed at any particular wavelength λ should be

$$(L_j^*)_\lambda = (L_j^*)_b\left(\frac{J_j}{J_i}\right)_\lambda\left(\frac{J_i}{J_j}\right)_b, \tag{13}$$

where the bolometric reflection $(L_j^*)_b$ is already known from section 4.

The value of $(J_i/J_j)_\lambda$ in equation (13) denotes the ratio of mean surface brightnesses of the illuminated hemispheres of both components, and if the system is an eclipsing variable it can be deduced at once from the rectified depths of both minima. The ratio of bolometric surface brightnesses $(J_i/J_j)_b$ does not follow directly from observations, and recourse must be had to a definite law of radiation. If our stars radiate like black bodies, then $(J_i/J_j)_b = (T_i/T_j)^4$, where the mean effective temperatures T of both components refer again to their illuminated hemispheres.[10] The factor

$$\left(\frac{J_i}{J_j}\right)_\lambda\left(\frac{T_j}{T_i}\right)^4 \tag{14}$$

is therefore always to be applied to the bolometric reflection in order to obtain its observable amount. Its value may, in practical cases, either exceed or be smaller than unity; and its

[9] This has first been pointed out by Eddington (*Royal Astron. Soc. Monthly Notices* **86**: 320, 1926) and subsequently elaborated by the writer (*Astrophys. Jour.* **89**: 323, 1939). Some of the formulae given in this latter paper were, unfortunately, obscure; they were later clarified in *Annals New York Acad. Sci.* **41**: 13, 1941.

[10] These are not likely to be identical with proper temperatures of the two components; for the heating effect of the incident radiation tends to equalize the temperatures of the illuminated hemispheres. Usually, however, temperatures corresponding to the spectra of the two components can be taken without much risk.

correctness depends only on how closely the actual stellar radiation comes to that of a black body. It is believed that for the present purposes the black-body law will provide an ample approximation.

II. Effects upon Radial Velocity

8.—An analysis of light variations invoked by the reflection effect being now complete, we proceed to investigate the effects of reflection upon radial velocities of components in spectroscopic binary systems. It is a well-known fact that the observed radial velocities can be regarded as wholly due to orbital motion only if the components are so far apart that their dimensions, expressed in terms of their separation, are negligible. If, however, the components are brought closer and can no longer be regarded as luminous points, their observed radial velocities continue to be purely orbital only if either the components possess no rotational momentum, or the distribution of brightness on their surfaces is uniform or radially symmetrical. So far as the present observational evidence goes, however, the components of close binary systems do seem to rotate—as a rule with considerable speed—about an axis which is perpendicular to the orbital plane or approximately so. Moreover, in the presence of reflected radiation the distribution of brightness on their surfaces cannot remain radially symmetrical. The center of light of the apparent disk of each component will no longer project itself constantly upon the center of mass, but will get displaced towards the source of incident light (that is, in the direction of the center of mass of the binary system), and its displacement will vary with the phase.

Thus the reflected light, coupled with rotation, is bound to produce radial-velocity changes which will superpose upon the orbital velocity of the rotating components. The amount of this contribution to the orbital velocity can be evaluated if we multiply the radial velocity at any surface point by the intensity of reflected radiation, integrate over the visible lune, and divide by the combined light (proper plus reflected) of the reflecting component.[11] In order to specify the problem, we again fix our attention on the primary component whose center of mass coincides with origin of our coordinate system, and assume it to rotate like a rigid body—an assumption justified on grounds of simplicity—with angular velocity ω_1 about an axis perpendicular to the orbital plane. The non-orbital velocity V' in the line of sight at any surface point of the primary star is then proportional to that point's distance from the apparent axis of rotation projected on the celestial sphere, and in the xy-coordinates introduced in section 4 it takes the form

$$V' = \pm\, \omega_1 r_1 \sin i(x \cos \eta - y \sin \eta), \quad (15)$$

where r_1 denotes the radius of the rotating primary in absolute units and η, the angle between the projected axis of rotation and the Y'-axis, is given by

$$\cos \eta = \sin \psi \csc \epsilon$$

and

$$\sin \eta = \cos \psi \cos i \csc \epsilon.$$

The sign of ω_1 in (15) is positive if rotation is direct, and negative if it is retrograde. Since no instance of retrograde rotation has so far been detected in close binaries, we shall hereafter work only with the positive sign.

The contribution δV to the radial velocity arising from rotation of the illuminated primary star is then given by

$$\left\{ \int_{-1}^{+1} \int_{0}^{\sqrt{1-y^2}} - \int_{-1}^{+1} \int_{0}^{-l_0\sqrt{1-y^2}} \right\} V' I r_1^2 dx dy, \quad (16)$$

divided by the primary's combined light $L_1 + L_1^*$. If the spectral lines of the reflecting star are to be visible, L_2 cannot be large compared with L_1. Hence L_1^* must be small in comparison with L_1; and as (16) itself is a small quantity of the order of $(r_1/R)^2$, it follows that L_1^* can be neglected in the denominator as far as terms of the order of $(r_1/R)^2$ or $(r_1/R)^3$ in δV are concerned. Integrating (16) to this order of accuracy and dividing by L, we obtain

$$\delta V = \frac{17}{16} \frac{L_2}{L_1} \left\{ \frac{1}{8} \left(\frac{r_1}{R} \right)^2 \sin \psi (1 + \cos \epsilon) + \frac{2}{15\pi} \left(\frac{r_1}{R} \right)^3 \sin \psi \sin \epsilon + \cdots \right\} \omega_1 r_1 \sin i. \quad (17.0)$$

[11] The velocities so defined will pertain to the centers of gravity of displaced spectral lines. The light reflected from rotating stars will render their lines asymmetrical (*cf.* McCarthy, *Astrophys. Jour.* **82**: 261, 1935; or Struve, *Astrophys. Jour.* **86**: 198, 1937); but unless the velocity of axial rotation is excessive, the measured Doppler displacements refer sensibly to the cores of asymmetrical lines.

The contribution to the radial velocity of the secondary component, due to light incident upon it from the primary, is also given by equation (17.0) if indices are interchanged and phase is shifted by 180°.

When, however, L_2 is large compared with L_1, the light reflected from the primary star may become comparable with, or even greater than, its own light. The neglect of L_1* in the denominator of δV is then inadmissible; in fact, if the reflecting star has little or no light of its own, the reflected light might represent its entire luminosity; in which case

$$\delta V = \frac{3}{8}\left\{\frac{\pi \sin\psi(1+\cos\epsilon)}{2(\pi-\epsilon)\cos\epsilon + 3\sin\epsilon} + \cdots\right\}\omega_1 r_1 \sin i, \quad (17.1)$$

correctly to a first approximation. The radial-velocity changes arising from axial rotation of a star shining only with reflected light are independent of intensity of the incident radiation and represent the maximum possible effect which the reflection can exert. All this may seem of only academic interest; for the spectrum of a dark star should ordinarily be invisible. Under special circumstances, however, the light reflected upon it may prove intense enough to record its lines in the combined spectrum. The spectrum of the reflected light should be characterized by its close resemblance to that of the bright star; in fact, it should probably be its replica in all features observed except in intensity, which should be small and should, moreover, undergo periodic fluctuation according to the phase of the reflecting star. The velocity curves derived from Doppler displacements of lines of the "reflected" spectrum would evidently possess a peculiar character, and a failure to consider the effects of reflection in a solution for orbital elements would lead to quite incorrect results.

Returning to equation (17.0), we notice that the ratio of luminosities L_2/L_1, and therefore δV, should apparently depend upon frequency of lines measured for radial velocity. On closer scrutiny, however, this proves not to be the case. For unless both components are of equal temperatures, the right-hand side of (17.0) is to be further multiplied by the factor (14), which accounts for the difference in observed efficiencies of the incident and reflected light. Since, however,

$$\frac{J_1}{J_2}\left(\frac{T_2}{T_1}\right)^4\frac{L_2}{L_1} = \left(\frac{r_2}{r_1}\right)^2\left(\frac{T_2}{T_1}\right)^4,$$

we see that the ratio L_2/L_1 in equation (17.0) refers in reality to the total luminosities of the two components and δV is therefore independent of wavelength.

9.—In order to investigate the significance of the foregoing results and their bearing upon the determination of elements of spectroscopic orbits, let us compare equations (17) with the radial velocity V of the primary component due to its orbital motion around the center of mass of the binary system. As is well known,

$$V = \gamma + K_1[e\cos\bar{\omega} + \cos(v+\bar{\omega})], \quad (18.0)$$

where γ denotes the systemic radial velocity; K_1, the semi-amplitude of the primary's velocity curve; e, the orbital eccentricity; v, the true anomaly in an eccentric orbit; and $\bar{\omega}$, the longitude of periastron measured from the ascending node. If the eccentricity is small, $v+\bar{\omega}$ can be conveniently expanded in terms of the mean anomaly M in a series whose first term, $\bar{\omega}+M$, gives the mean longitude which we shall hereafter denote Ω. To the first order in e, equation (18.0) can be rewritten as

$$V = \gamma + K_1\cos\Omega + K_1 e\sin\bar{\omega}\sin 2\Omega + K_1 e\cos\bar{\omega}\cos 2\Omega + \cdots. \quad (18.1)$$

To this order of accuracy

$$K_1 = \frac{m_2\sin i}{m_1+m_2}\mu R, \quad (19)$$

where m_1, m_2 denote the masses of the two components and μ stands for the mean daily motion. If the orbital eccentricity is zero or small, it is reasonable to assume that the components rotate in the same period as they revolve[12]—in which case the angular velocity ω_1 in equations (17) can be put equal to the mean motion μ. Since, furthermore, $\Omega = \psi + 90°$, equation (17.0), rewritten in terms of Ω to the first approximation, takes the form

$$\delta V = -\frac{17}{128}\frac{L_2}{L_1}\left(1+\frac{m_1}{m_2}\right)\left(\frac{r_1}{R}\right)^3 K_1 \times\left\{\cos\Omega + \frac{1}{2}\sin i\sin 2\Omega\right\} + \cdots. \quad (20)$$

[12] *Cf.* Kopal, *Harvard Circ.* 443 (sec. 3), 1940.

Equation (17.1), rewritten similarly, becomes considerably more complex; but since it is valid only in a very special case, we shall not discuss it in the same detail.

Now the observed radial velocity of the reflecting star is $V + \delta V$. If, therefore, its observed velocity curve is solved for elements of the spectroscopic orbit in the usual manner—without regard to reflected light—a comparison of equations (18.1) and (20) reveals that some elements will be systematically in error. First, in the presence of reflected radiation the observed coefficient of cos Ω will not be K_1 as in idealized equation (18.1), but

$$\left\{1 - \frac{17}{128}\frac{L_2}{L_1}\left(1 + \frac{m_1}{m_2}\right)\left(\frac{r_1}{R}\right)^3 + \cdots\right\} K_1, \quad (21.0)$$

if L_2 is not large compared with L_1, and

$$\left\{1 - \frac{\pi}{8}\frac{r_1}{R} + \cdots\right\} K_1, \quad (21.1)$$

if the primary component shines only with reflected light (and consequently m_1/m_2 is small). The reflection therefore tends to diminish the observed radial-velocity amplitudes by a small but definite amount. The measured values of K_1, reduced without regard to reflected light, are thus necessarily underestimated; and so are the mass-functions and masses of the stars derived therefrom.*

Second, the term in (20) varying as sin 2Ω will evidently simulate orbital eccentricity. A comparison of equations (18.1) and (20) reveals that the effects of reflection upon velocity curves of close binary systems are such as to lead the orbit computer to a slightly eccentric orbit specified by

$$e = \frac{17}{256}\frac{L_2}{L_1}\left(1 + \frac{m_1}{m_2}\right)\left(\frac{r_1}{R}\right)^3 \sin i, \quad (22)$$

and $\bar{\omega} = 270°$ even if there were no real eccentricity at all. On the other hand, if the orbit is not really circular, we should expect the spurious e arising from reflection to combine with the real orbital e to yield a resultant which may be either smaller or larger than the real e. Under special conditions the effect, upon radial velocities, of a real but small orbital eccentricity could be masked completely by the reflection effect. Furthermore, in dealing with two-spectra binary systems we have to bear in mind that the spectroscopic values of e and $\bar{\omega}$, specifying the absolute orbits of both components and deduced from the observed velocity curves without regard to reflected light, will generally not be identical. In particular, if the orbits are really circular, the spurious $\bar{\omega}$'s relative to both components should differ by 180°.

10.—In order to illustrate the relative importance of results derived in preceding sections, let us carry out an application to μ^1 Scorpii and u Herculis as numerical examples. Both these stars are typical representatives of two-spectra eclipsing systems with components of comparable luminosities to which equation (20) can safely be applied. According to Struve,[13] the observed semi-amplitudes of the velocity curves of components of μ^1 Scorpii are $K_1 = 185$ km/sec and $K_2 = 280$ km/sec. Since, according to Rudnick and Elvey,[14] $L_2/L_1 = 0.8$, $r_1/R = 0.3$, $r_2/R = 0.4$, and $i = 61°$, (21.0) shows that the true semi-amplitudes, corrected for reflection, are $K_1 = 186$ km/sec and $K_2 = 285$ km/sec. Hence the masses m_1, m_2 of the components, as derived by Struve from uncorrected semi-amplitudes, are underestimated by 2 and 6 percent, respectively. In the case of u Herculis the observed semi-amplitudes are $K_1 = 100$ km/sec and $K_2 = 253$ km/sec.[15] Since, according to Baker,[16] $L_2/L_1 = 3/7$, $r_1/R = r_2/R = 0.3$, and $i = 78°$, the true semi-amplitudes result $K_1 = 101$ km/sec and $K_2 = 256$ km/sec, and hence the masses m_1, m_2 of the two components are in reality greater than those given by Baker by 2 and 4 percent, respectively. In view of the crudity of adopted data, the above figures for effects of reflection upon semi-amplitudes of the radial-velocity curves of μ^1 Scorpii and u Herculis are admittedly rough estimates, but are certainly of correct order of magnitude. In either system these effects are found to be quite small—possibly at the limit of significance—and are likely to be equally small in all similar binaries.

The same applies to the spurious eccentricities invoked by reflection. If the above data pertaining to μ^1 Scorpii and u Herculis are inserted

* This was in fact qualitatively anticipated by Eddington (*Royal Astron. Soc. Monthly Notices* **86**: 320, 1926).

[13] *Astronomical papers dedicated to E. Strömgren*, p. 258. Copenhagen, 1940.

[14] *Astrophys. Jour.* **87**: 553, 1938.

[15] *Allegheny Publ.* **1**: 33, 1908 (re-discussed by Sterne, *Proc. Nat. Acad. Sci.* **27**: 175, 1941).

[16] *Lick Observ. Bull.* **12**: 130, 1926.

in equation (22), the spurious eccentricities of absolute orbits of their components result $e_1 = 0.004$, $e_2 = 0.008$, and $e_1 = 0.003$, $e_2 = 0.006$, respectively. The corresponding longitudes of periastra (reckoned from the ascending node of each velocity curve) are 270°. It should be noted, however, that the spectroscopic eccentricities in close binary systems are likely to be further vitiated by effects, upon radial velocities, arising from limb- and gravity-darkening over surfaces of tidally distorted components. Such effects have recently been quantitatively investigated by Sterne.[17] The spurious tidal eccentricity was found to be of the order of $(r_1/R)^4$ and the longitude of periastron usually (though not always) equal to 90°. If so, the eccentricity-simulating effects of ellipticity and reflection will evidently tend to cancel. Numerically, for data relative to μ^1 Scorpii Sterne's formula yields $e_1 = 0.004$, $e_2 = 0.017$; while in the case of u Herculis $e_1 = 0.003$[18] and $e_2 = 0.008$. The longitude of periastra of fictitious ellipses invoked by the ellipticity and reflection differ by 180°; hence the "effective" spurious eccentricity will be a difference of the tidal and reflection eccentricity. Subtracting the values found above, we find that only for μ^1 Scorpii B the effective spurious e may be as large as 0.01; while spurious eccentricities of μ^1 Scorpii A or of both components of u Herculis should be of the order of 0.001 or even smaller.

Now the spectroscopic eccentricity of absolute orbit of u Herculis A was found to be 0.053 $\pm$ 0.009 (p.e.) and the longitude of periastron $\tilde{\omega} = 93° \pm 10°$.[19] A recent discussion by Martin[20] of extensive photometric material relative to u Herculis has shown, however, that this spectroscopic eccentricity is apparently spurious; for the light curve is definitely inconsistent with any value of e exceeding 0.01. This is not an isolated instance of an eclipsing system where the spectroscopic eccentricity comes out too high or seems wholly spurious, and the longitude of periastron is in the vicinity of 90°. Moreover, it has been noticed long ago that the longitudes of periastra of spectroscopic binaries are not distributed at random in space, but tend to cluster around 90°—a fact for which no satisfactory explanation has ever been given. The results of the present investigation seem to dispose of the possibility that the effects, upon radial velocities, of ellipticity or reflection could be responsible for it. The rotation of gravity-darkened ellipsoids simulates in fact a spuriously eccentric orbit with the longitude of periastron of 90°, but this effect, small as it is, will in practical cases be largely masked by equally spurious eccentricity arising from reflection, which leads to $\tilde{\omega} = 270°$. The net outcome of the eccentricity-simulating effects of ellipticity and reflection will as a rule be minute; and the spurious spectroscopic eccentricity in u Herculis and similar eclipsing variables as well as the clustering of longitudes of periastra of spectroscopic binary systems in the neighborhood of 90° remain therefore unexplained.

The question may be asked: Is there any escape from these conclusions? There is one point which may be stressed in this connection. In passing from equation (17.0) to (20), we assumed that the reflecting star rotates with the Keplerian angular velocity. If its actual rotation is n-times the mean daily motion, δV, and therefore also (21) or (22), should be theoretically n-times magnified. In practice, however, this proportionality may not be rigorously fulfilled, since fast rotation (in a period short compared with that of the orbit) might be expected to reduce the magnitude of observed reflection effect and introduce a displacement in phase, with complete disappearance of both as a limit.[21] Furthermore, it is unlikely that components of binary systems as close as μ^1 Scorpii or u Herculis could rotate much faster than they revolve. But even if they do, the spurious eccentricities arising from ellipticity and reflection would be equally increased; and since only their difference is observable, the net outcome would continue to be small. Hence it does not seem likely that an eventual breakdown of synchronism between rotation and revolution could materially alter our former conclusions.

Summarizing briefly the results of the fore-

[17] *Proc. Nat. Acad. Sci.* **27**: 168, 1941.

[18] Sterne (*op. cit.*) gave $e_1 = 0.013$. This value appears, unfortunately, to be in error owing to the fact that Sterne, in estimating the distortion of u Herculis A, identified the mean photometric ellipticity of the system (due largely to its less massive secondary component) with that of the primary star.

[19] *Cf.* Sterne, *Proc. Nat. Acad. Sci.* **27**: 175, 1941.

[20] *Bull. Astron. Inst. Netherlands* **8**: 265, 1938.

[21] A suggestion due to Russell (*cf.* Pike, *Astrophys. Jour.* **73**: 212, 1931).

going paragraphs, we conclude that a harmonic analysis of observed velocity curves of close binary systems should always yield a term varying as sin 2Ω. If the true orbit is circular, the coefficient of this term should be small, as a rule, and admit of an easy interpretation; while if the true orbit is eccentric, the situation may become too complex to be analyzed in simple terms. The contributions to the radial velocities arising from both the ellipticity and reflection should then be applied[22] to the observed velocities before a conventional orbital solution is carried out; for only then elements may be obtained that are reasonably free from any obvious source of systematic errors.

[22] This is individually possible only for eclipsing systems where all quantities constituting δV can be determined from an analysis of their light curves. In non-eclipsing spectroscopic binaries the magnitude of some factors can only be estimated.

THE ORBITAL MOTION OF 61 CYGNI

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THE present investigation is part of a program which was started by the writer at the University Observatory in Leiden, Holland, in 1933.

The plan was to determine orbital motions for a number of double stars for which sufficient accurate photographic observations were available to make special use of such material. Since then ten systems have been investigated, of which 61 Cygni is one.

Before discussing the motion in 61 Cygni, a short account will be given of the photographic observations. The method was developed by the Danish astronomer Hertzsprung at the Potsdam Observatory in Germany during the years 1914–19.

Photographs of the double stars are taken with a visual telescope with a large focal length. The developed plate, with as many as 60 images on it, is measured in a machine with a high-precision screw. The work exceeds greatly that involved in the conventional method of obtaining visual observations of double stars, but an accuracy of as much as ten times the best visual observations is obtained, provided certain precautions have been taken. Moreover, in contrast to the visual observations, we have in the plates permanent documents which can be measured again years after they were taken.[1,2,3]

Hertzsprung's work was discontinued when he left Germany in 1919, and except for a limited number of plates taken by him and his associates during his visits to Johannesburg in South Africa and to the Lick Observatory in California, no further attempts were made to carry on an extensive program until the initiation of the program at Swarthmore College in November, 1938. Since then more than 500 plates have been taken with the 24-inch Sproul refractor over a period of four years, and more than a quarter-million settings were made at the measuring machines. I can truthfully say that the Sproul telescope has proven itself an excellent instrument for this kind of work.

The investigation of the motion in the ten stellar systems has led to the discovery of invisible stellar companions in three of the systems, while a planetlike companion was found in another system.

The first six orbits published[2] were for the stars η Cassiopeiae, γ Virginis, ξ Bootis, σ Coronae Borealis, 44i Bootis, and 70 Ophiuchi; Hertzsprung's early plates and additional material from Potsdam and Johannesburg (1929–1935) were used. None of the stars showed any deviation from Kepler motion, and conclusive proof was given that the anomalies shown by the visual observations of 70 Ophiuchi were due to systematic errors in the visually observed distances, changing with the components' apparent separation.

For each of these stars (excepting 44i Bootis on account of the present small separation) several plates have been taken at each opposition with the Sproul refractor. This additional material confirmed the previous results of unperturbed orbits, except for ξ Bootis where a perturbation was found having a period of approximately two years.[4] The third component has a mass of 1/10 that of the Sun and moves in an apparent orbit which is nearly a straight line.

No perturbation was found for α Geminorum,[5] already known to be a sextuple system, while for ζ Aquarii,[6] and μ Draconis[7] stellar companions with masses approximately half that of the Sun were found.

61 Cygni, of which a more detailed account is now given, was found to have a planetlike companion with a mass of about 16 times that of Jupiter. 61 Cygni is a wide double star with such a slow orbital motion that the 28 years covered by the very accurate photographic

[1] Hertzsprung, E., *Publ. Astrophys. Observatorium Potsdam* 75, 1920.

[2] Strand, K. Aa., *Annalen Sterrewacht Leiden* **18** (2), 1938.

[3] Strand, K. Aa. Photographic measurements of double stars. *Sky* **5**: 6–8, 1941.

[4] Strand, K. Aa., *Publ. Astron. Soc. Pacific* **55**: 28–29, 1942.

[5] Strand, K. Aa., *Astron. Jour.* **49**: 41–49, 1940.

[6] Strand, K. Aa., *Publ. Astron. Soc. Pacific* **53**: 247–248, 1941; *Astron. Jour.* **49**: 165–172, 1942.

[7] Strand, K. Aa., *Publ. Astron. Soc. Pacific* **55**: 26–28, 1942.

observations form entirely too short an interval to determine the orbit. Additional observations were therefore necessary. Very important additions were the results from photographs taken by Mr. Lewis Rutherfurd in his private observatory with a 13-inch telescope (13-foot focal length) in the years 1870 to 1874.[8] The 19 plates of this special object are all well preserved and were kindly loaned to us by Dr. Jan Schilt, director of the Rutherfurd Observatory of Columbia University. The plates were measured in the same way as the modern material and gave very satisfactory results. A further extension of the observational material was obtained by using visually observed position angles, which from previous investigations were believed free from systematic errors in contrast to the visually observed distances.[9]

In this way material was at hand covering about 110 years.

No detailed discussion will be given of the elaborate computations needed for a full discussion of the determination of the orbit. About 30 different orbits with periods varying from 550 to 1,100 years were computed. The analysis of these computations is not yet finished, but an orbit with a period of 720 years, eccentricity of .40, and a semi-axis major of 24".554, agrees very well with the observations.[10]

[8] Davis, Herman S., *Contr. Observatory Columbia University, New York*, 12, 13, 1898.

[9] Van de Kamp, Peter, *Am. Philos. Soc. Year Book* 1941: 95–96, 1942.

[10] Strand, K. Aa., *Publ. Astron. Soc. Pacific* **55**: 29–32, 1942.

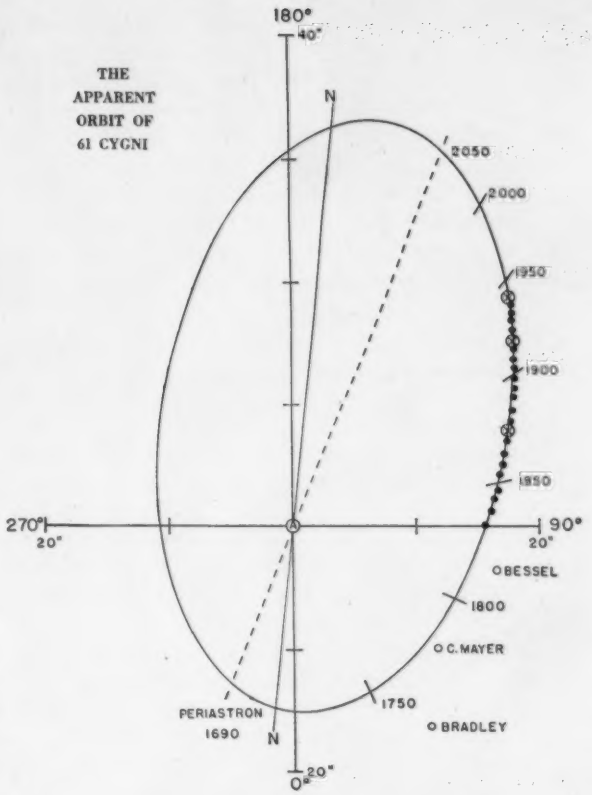

FIG. 1. The ellipse shows the computed apparent motion of the faint component with respect to the bright component at A. The true orbit is inclined 52 degrees around the line of the nodes, N–N.

What we observe is the projection on a plane vertical to the line of sight as shown in figure 1.

TABLE 1

THE ORBITAL MOTION OF 61 CYGNI

Epoch	X	(m.e.)	Y	(m.e.)	Residuals: Triple system		Residuals: Double system		Plates
1914.670	+18".048	±".005	−14".952	±".005	+".006	+".004	−".003	+".010	7 Potsdam
15.700	.040	6	15.116	6	− 7	+ 4	− 5	+ 10	5 Potsdam
16.727	.053	7	.283	7	+ 4	+ 2	+ 15	+ 6	4 Potsdam
17.627	.025	9	.433	8	0	+ 1	− 6	0	2 Potsdam
18.729	.002	6	.603	7	− 5	+ 1	− 21	+ 5	3 Potsdam
35.496	17.798		18.193		+ 4	− 14	+ 8	− 8	2 Potsdam
37.665	.735	4	.500	4	+ 5	+ 4	− 11	+ 5	5 Lick
39.667	.696	5	.792	5	− 4	0	− 8	+ 6	4 Sproul
40.609	.691	4	.932	4	+ 2	− 4	+ 8	+ 2	6 Sproul
41.571	.668	3	19.066	3	− 5	+ 8	+ 7	+ 10	6 Sproul
42.606	.620	4	.221	4	− 2	− 3	− 18	− 2	3 Lick
Median error	±".005$_5$				±".006		±".010		

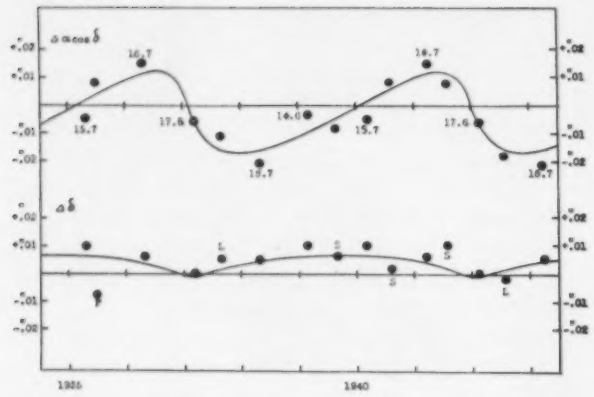

FIG. 2. The residuals: observed minus computed, in right ascension and declination, left by the long period orbit of 61 Cygni.

Dots represent means of visual observations for five years; crosses are photographic observations. The early observations made by Bradley, Bessel, and Mayer do not possess any high degree of accuracy. The apparent dimensions of what we observe are illustrated by the fact that 20″ are about 1 mm. (1/25 inch) on the photographic plate. The actual dimensions are obtained if we use the parallax of ″.294 or 11.1 light years based on modern observations. The present separation of the components is then about 110 times that between the Earth and Sun. Since we know the mean distance to be 84 astronomical units, and the period 720 years, we obtain from Kepler's third law a total mass of the system of 1.16 times that of the Sun.

An inspection of the residuals from the elliptic motion shows marked periodic deviations in the photographic observations (fig. 2), especially in the $\Delta\alpha \cos\delta$ coordinate. The period of this variation was found to be 4.9 years, and the curves were obtained from an ellipse with a semi-axis major of ″.02 and an eccentricity of 7/10. The observations after 1935 are plotted with their proper epochs, while Hertzsprung's results from 1914 to 1919 have been plotted after the addition of a whole number of periods to their epochs. The scale of the perturbations is so small that only the accurate photographic observations can reveal them.

The observed values are given in the table. Each yearly mean consists of several plates. If a perturbation of the nature just mentioned is accounted for, we obtain the first set of residuals. It is seen that the agreement between observed and computed motion is very satisfactory, since the residuals give an error equal to the internal error. Without accounting for a perturbation, the residuals become too large, as indicated by the median error of ″.010.

The extent of material can be judged from the fact that altogether more than 34,000 settings were made to obtain the results.

With the secondary ellipse superimposed upon the first ellipse, we get the motion shown for a short interval in figure 3. The dotted line corresponds to a short arc of the ellipse in figure 1. The star is actually following the full drawn line.

The perturbation thus revealed by the photographic observations shows that the system, besides its two visible components, has a third member which we cannot see, but whose presence is revealed by its gravitational attraction upon one of the visible components as it travels around it. The only solution which will satisfy the

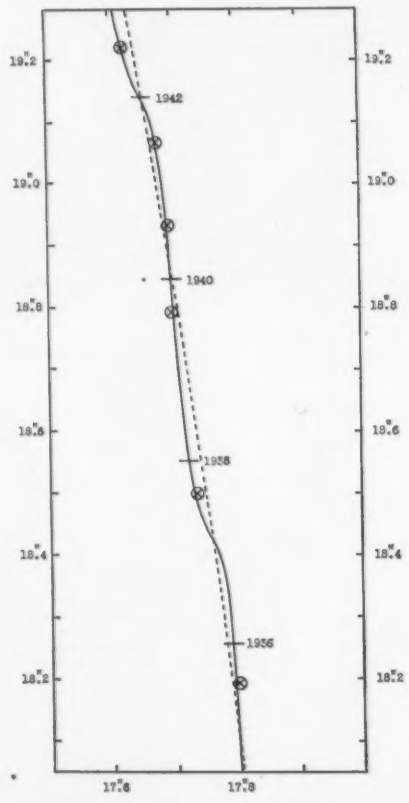

FIG. 3. The orbital motion of 61 Cygni from 1935 to 1943 on a scale 50 times that of the complete orbit. This enlarged section of the orbit illustrates the superior accuracy of the photographic observations. The yearly means of the photographic positions (×) deviate very little from the computed orbit.

observed motion gives the remarkably small mass of 1/60 that of our Sun or 16 times that of Jupiter, for the third member. This is considerably smaller than the smallest known stellar mass, which is 1/7 that of the Sun. We have reason to believe that a celestial body with such small mass must have such an extremely low intrinsic luminosity that we may consider it a planet rather than a star. This would mean that we have found the first case of planetary motion outside our solar system.

In conclusion, a short description of the system will be given. 61 Cygni is 11 light years away from us and thus one of our Sun's closest neighbors. There are two visible components which are red dwarf stars, each having a mass of 6/10 that of our Sun. They revolve around each other once in 720 years, and their present separation is about 110 times that between the Earth and the Sun.

Besides these two members there is a third, invisible member, which has a mass of only 16 times that of Jupiter, so that we have reason to believe it to be a planet. It travels in an eccentric orbit around one of the visible components with a period of five years, and has a mean distance from it of twice that between the Earth and the Sun. The apparent motions in the large and small orbits are in the same direction; the true orbits, however, are highly inclined against each other in contrast to the case of the Sun and its planets.

It is a great pleasure to acknowledge a grant from the Penrose Fund of the American Philosophical Society in carrying out this investigation.

THE GLACIAL ANTICYCLONE AND THE CONTINENTAL GLACIERS OF NORTH AMERICA

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(*Read November 21, 1942*)

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HISTORICAL

Mountain Glaciers the Model in the Past Study of Continental Glaciers

MORE than a century ago, when Louis Agassiz found in Great Britain deposits of till and striated erratic boulders such as he had observed about small mountain glaciers in Switzerland, he founded his theory of an earlier European glacier on a continental scale. The assumed properties of this continental glacier, except for size and outline, were those of the Swiss glaciers. When he visited the United States a few years later, evidence for another and similar blanketing continental glacier was discovered.

Of the two existing continental glaciers which lie within the Arctic and Antarctic regions, neither had been visited by a student of glaciers.

It was to be a full half-century before the Greenland glacier would be brought under observation, and even longer before the Antarctic would be examined.

In the meantime the work of the Pleistocene glaciers of both North America and Europe had been studied in considerable detail, but, naturally, with the picture of the small Swiss glacier in the mind and supplying the model. Erosion, transportation, and deposition were believed to have been by the ice itself through a sort of flow almost throughout its extent, but with thaw-water action under its near front and within the extrafrontal (periglacial) area, and with glacial debris carried down such river valleys as flowed away from the glacier front.

Conditions Observed over and around the Greenland Continental Glacier

Of the two existing continental glaciers, that of the Antarctic spreads out so as completely to overwhelm the continent. As a consequence there is in the Antarctic no periglacial area which could be studied. In Greenland a periglacial area exists, but not in the region where late in the nineteenth century the early glacial studies were undertaken, first by T. C. Chamberlin[1] and a little later by Salisbury.

For the glacier itself a great explorer, Peary,[2] had already discovered a previously unknown property. It had to do with the nature of the wind above the ice. Fierce storm winds throughout the areas traversed were found during two complete and other partial transections of the glacier to move outward centrifugally from the central area of the flat-domed ice surface, very much as water would do under the same gravitative action.

Vastly important as was this discovery, for a full quarter-century it in no way modified the views of glacialists concerning either existing or earlier glaciations. Study of the narratives of other Greenland explorers revealed that this glacier is overwhelmed by an anticyclonic air circulation of its own making, which spreads out from its margins centrifugally over the periglacial zone. This glacial anticyclone oscillates from periods of relative calm to a fierce storm system with extreme wind velocities in excess of 150 miles per hour.[3]

Over the Antarctic glacier there prevails an anticyclonic circulation of almost identical pattern but even greater intensity, in correspondence with its thrice greater magnitude.[4] Of similar nature, though not so persistent and of far less intensity, are anticyclonic circulations over the inland ice of Northeast Land (Svalbard) and over some of the ice caps of Iceland.

The Periglacial Zone of the Greenland Glacier

The glacial anticyclone of Greenland spreads outward over a periglacial zone, the width of which has not been accurately determined, though certainly it is more than 100 miles. It was not until this zone had been studied within the Holstensborg district of southwest Greenland that the role of the glacial anticyclone in erosion,

FIG. 1. View of a part of the former plain of outwash of the Greenland continental glacier, now elevated, at the head of the Söndre Strömfjord, West Greenland. Note the stranded boulders drilled by the sand blast. (Photo by W. H. Hobbs.)

[1] Chamberlin, T. C. Glacial studies in Greenland. *Jour. Geology* **2–5**, 1894–1897.

[2] Peary, Robert E. A reconnaissance of the Greenland inland-ice. *Jour. Am. Geog. Soc.* **19**: 261–289, 1887.
—— Journeys in North Greenland. *Geog. Jour.* **11**: 233–234, 1898.
—— *Northward over the Great Ice* **1**: lxix–lxx, 1898.

[3] Hobbs, W. H. Characteristics of the inland-ice of the Arctic regions. *Proc. Am. Philos. Soc.* **49**: 57–129, 1910.
—— *Characteristics of existing glaciers*, chs. viii–x, 1911.
—— The role of the glacial anticyclone in the air circulation of the globe. *Proc. Am. Philos. Soc.* **54**: 185–225, 1915.

[4] Hobbs, W. H. The ice masses on and about the Antarctic continent. *Zeitschr. Gletscherkunde* **5**: 36–122, 1910.
—— *Characteristics of existing glaciers*, pp. 261–289, 1911.
—— *The glacial anticyclones, the poles of the atmospheric circulation.* New York, 1926.

transportation, and deposition came to be known. With the model of mountain glaciers as a guide, it had been assumed that the sole agent of these processes within the periglacial zone of continental glaciers was running water, which progressively builds up the outwash apron from materials shaped and contributed by the glacier itself.

Observations made by the Greenland expeditions of the University of Michigan have now shown that water transportation within the periglacial area is restricted to the brief warm season of a few months only, and that during the remaining months of the year the fierce winds of the glacial anticyclone take over completely the processes of transportation, erosion, and deposition. During the brief summer season the role of the melt-water is much greater than had been supposed, for ice blocks detached from the lower levels of the glacier front, burdened as these are with englacial rock material of all sizes up to boulders several feet in diameter, are floated for long distances. During a summer day, and with rain, so much thaw-water sometimes forms as to flood large portions of the outwash area to a depth of a number of feet. At such times the ice blocks are drifted over portions of the plain of outwash and become stranded upon it as the flood subsides. Melted, these blocks leave their boulders and smaller rock debris upon the plain (see figs. 1, 4, and 5). Other bergs are restricted in their movements to the braided channels within the plain, and their included boulders either are carried to greater distances on the plain or become entombed in its deposits.

With the close of the warmer season, melting of the glacier comes to an end, and under the unsaturated katabatic winds off the ice the plain of outwash rapidly dries out. No longer held down by its included water, the finer rock material of its surface layer (silt, sand, and the smaller pebbles) is lifted by the strong winds of the anticyclone and carried off, the silt as dust to be spread far and wide and laid down as loess deposits wherever there is vegetation, and the sand to be built up either into sand hills within some eddied area (see fig. 3) or into elongated dunes which by reason of the violence of the storms are usually parallel to the wind, or nearly at right angles to the glacier front. Of the surface deposits there is left behind a layer of coarse pebbles only, since these are too heavy for the wind to carry off. Thus is formed a "pebble pavement" to the plain, similar to the *sêrir* of the Libyan desert or the "gibber plain" of arid Australia. (See fig. 2.)

FIG. 2. Pebble pavement of part of the uplifted outwash plain of the Greenland glacier. At head of the Söndre Strömfjord. (Photo by W. H. Hobbs.)

FIG. 3. Hill of eolian sand near head of the Söndre Strömfjord, West Greenland. (Photo by W. H. Hobbs.)

The sand, while carried in the air near the ground, is driven against the boulders exposed on the plain and against any other projecting rock masses, so that these become drilled by the bombardment. If of non-homogeneous material, and especially if they include small dikes or veins of more resistant material, the boulders are transformed into ribbed or recessed rocks or "stone lattices" so common in the deserts of lower latitudes (see figs. 1, 4, and 5). Each summer season these boulders are shoved about, rotated, and overturned by floating ice blocks and the swirling currents about them, and so with each succeeding winter they present new faces to the sand blast. Fine-grained homogeneous rocks and especially quartzite under strong sand blast are known from studies in other parts of the world to yield the familiar facetted ventifacts, the so-called windkanter (*einkanter*, *zweikanter*, or *dreikanter*), but such rock types are absent from

FIG. 4.

FIG. 5.

FIGS. 4 and 5. Ribbed or recessed boulders shaped by the sand blast on a raised outwash plain of the Greenland glacier. Head of Söndre Strömfjord, West Greenland. (Photos by W. H. Hobbs.)

the area studied in Greenland. The photograph of a fine example from Iceland is shown in figure 6. The winter conditions about a continental glacier are desert conditions, and except for the prevailing lower temperatures and the presence of winter snow not greatly different from those of the tropical deserts.[5]

[5] Hobbs, W. H. Loess, pebble bands and boulders from glacial outwash of the Greenland continental glacier. *Jour. Geology* **39**: 381–385, 3 fig., 1931.

Kay, George F. Origin of the pebble band on Iowan till. *Jour. Geology* **39**: 377–380, 1931.

Hobbs, W. H. The origin of the loess associated with continental glaciation, based upon studies in Greenland. *Cong. Intern. Géographie Paris, 1931, Comptes Rendus* **2**, f. 1: 408–411, 1933.

—— Conditions at the front of a retreating ice-sheet. *Papers Michigan Acad. Sci., Arts and Letters* **25**: 477–480, (1939) 1940.

Prior to the studies made within the Holstensborg region of Greenland, no satisfactory explanation had been found for the widespread deposits of loess which are associated with the continental glaciers of the past. Such deposits are now seen to have been laid down by the winds blowing off the glaciers themselves and so are of contemporaneous formation. Heretofore also it has been necessary to call in a submergence of the land by the sea and a subsequent elevation, or a frontal glacier lake, whenever boulders have been found laid down beyond the limits of the till deposits. The floating ice necessary for this forward movement of the boulders no longer requires an invasion by the sea, or the presence of glacial lakes, but only the usual summer floodings of the outwash plain by glacier thaw-water.

These conditions revealed by study of the Greenland glacier canot be confirmed from the Antarctic region, since no periglacial land area has been uncovered there. The pronounced sand-blast effects of the operation of the glacial anticyclone have, however, been abundantly displayed on the nunataks of the glacier itself.[6]

Early Observations of Intense Wind Action about Pleistocene Continental Glaciers

The conditions revealed within the periglacial area of Greenland require a restudy of the Pleistocene continental glaciers of North America and Europe, and since the periglacial areas during one ice invasion have been overridden by the

FIG. 6. Facetted ventifact from the periglacial area of a Pleistocene ice cap in Iceland. (Photo by André Cailleux.)

[6] Scott, R. F. *The voyage of the "Discovery"* **2**: 466, pl. opp. p. 450, 1905.

Huxley, L. (ed.). *Scott's last expedition* **2**: 80, 1913.

glaciers of later invasions, as well as during advances and retreats of the same glacier, this means a survey of the entire glaciated area, for boulders which reveal sand-blast effects may be picked up from the outwash to become involved in the later morainic deposits. The loess from each ice invasion may be spread out over much if not all of the deposits from earlier glaciations as well as beyond their borders, and for more limited areas the sand accumulations as well.

Obviously the role played by floating ice over the outwash area helps solve an old puzzle, namely, the occurrence of glacial erratics found far outside the limits of the till deposits, as for example in New Jersey and elsewhere. Likewise the dunes of sand built up far from the sea over recognizable glacial deposits and with an orientation not explainable in prevailing winds of today, now no longer offer difficulties of interpretation.

Facetted Ventifacts within the Glaciated Area of North America

So soon as we look for the evidences of intensive wind action within the areas of North American and European glaciations, they are found in such abundance we are surprised that they had not before forced themselves more widely upon the attention of students of glaciation.[7] As a matter of fact, they were early discovered within both regions, but not being explainable in accepted theories, they attracted little attention.

FIG. 7. Boulders on "Iowan" outwash plain, one near right a recessed ventifact. The locality is 100 miles from the Des Moines lobe, and west of Troy Mills, Linn County, Iowa. (Photo by W. H. Hobbs.)

[7] Hobbs, W. H. The Pleistocene glaciation of North America viewed in the light of our knowledge of existing continental glaciers. *Bull. Am. Geog. Soc.* **43**: 641–659, 1911.

FIG. 8. Ribbed or recessed ventifact on campus of Depauw University at Greencastle. Found at Morton, Indiana. The ellipsoidal form is typical. (Photo by Ernest Smith.)

As far back as 1879 Stone found that boulders from the drift of Bethel and neighboring localities in southwestern Maine were not to be distinguished from those shaped by intensive wind action in deserts.[8] A few years later Shaler[9] reported similar boulders from Nantucket, and Salisbury[10] other examples from various localities where they were found associated with glacial outwash. Woodworth[11] reported many facetted wind-shaped pebbles from the drift of eastern Massachusetts, about Narragansett Bay and on Martha's Vineyard, and these observations were later confirmed by other observers.[12] Winchell[13] contributed a locality from Michigan, Clarke[14] from the Gulf of St. Lawrence, and Alden and Leighton[15] from Iowa.

[8] Stone, G. H. Wind action in Maine. *Am. Jour. Sci.*, ser. 3, **31**: 133–138, 1886.

[9] Shaler, N. S. The geology of Nantucket. *U. S. Geol. Survey Bull.* 53: 21–26, 1889.

[10] Salisbury, R. D. *Ann. Rept. State Geologist New Jersey* **1892**: 155, 1893.

[11] Woodworth, J. B. Postglacial eolian action in southern New England. *Am. Jour. Sci.*, ser. 3, **47**: 63–71, 1894.

[12] Shaler, N. S., G. K. Gilbert, and W. M. Davis. *Am. Geologist* **13**: 146–147, 1894.

Davis, W. M. Facetted pebbles on Cape Cod, Mass. *Proc. Boston Soc. Nat. Hist.* **26**: 166–176, pls. I–II, 1894.

[13] Winchell, A. *Geological studies* [etc.], p. 284. Chicago, 1892.

[14] Clarke, John M. Notes on the geology of the Gulf of St. Lawrence. *New York State Mus. Bull.* 149: 121–133, pls. II–IV, 1911.

[15] Alden, William C., and M. M. Leighton. The Iowan drift [etc.]. *Iowa Geol. Surv.* **26**: 153 (1915) 1917.

Facetted Ventifacts from the Pleistocene Glaciation of Europe

From the area of the Pleistocene glaciation in Europe many examples of facetted wind-etched boulders were early reported. In 1884 Wahnschaffe drew attention to windkanter from the diluvial sand near Züllichau in Saxony.[16] In 1884 there appeared also a most important paper by Berendt.[17] He had as early as 1876 laid before a meeting of the German Geological Society a collection of perfectly shaped dreikanter not to be distinguished from desert forms, but which had all been collected from the widely extended outwash plain about Berlin, or from other similar outwash deposits of northern Germany. On the basis of this publicity, eight other geologist colleagues extended the localities for dreikanter within the German glacial deposits. Some of the localities were Stendal and Gardelugen in the valley of the Elbe; others were found near Hamburg, Connern, Mecklenburg, Stolpen in Saxony, Schonen, and Lyons in France. In size these boulders varied from that of a man's fist to head size. Though these ventifacts were clearly associated with glacial deposits and generally outwash, no satisfactory theory of their origin was set up. Interaction of boulders under water was the explanation offered.

In 1888 von Mickwitz[18] and in 1914 Reitz[19] supplied new localities for facetted ventifacts from the European drift deposits. More recently Dücker[20] and Cailleux[21] have published the results of extended studies on facetted ventifacts from the European glacial deposits. The aggregation of these dreikanter in groups or nests both geologists explained by association with solifluction, which is so generally present in Arctic regions, elevates the boulders out of their deposits, and is believed to be connected in its origin with alternate freezing and thawing.

From the drift deposits of the British Isles dreikanter were early reported by Bather.[22] Jackson[23] also discussed such ventifacts from the glacial deposits of Lancashire and Cheshire, but he felt compelled to assign their origin to postglacial time. Others, including Wills,[24] have reported them.

FIG. 9. Recessed ventifacts on campus of Oberlin College, Oberlin, Ohio. (Photo by George D. Hubbard.)

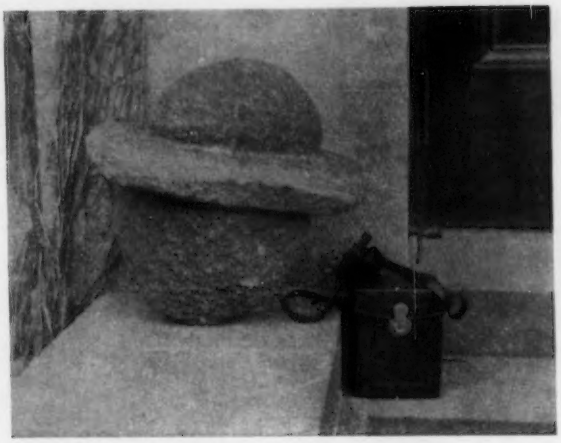


FIG. 10. Recessed ventifact on campus of the University of Michigan at Ann Arbor. Near aplite dike indication of rebound of sand grains. (Photo by I. D. Scott.)

[16] Wahnschaffe, F. *Zeitschr. Deutsch. Geol. Gesell.* **36**: 411, 1884.

[17] Berendt, G. Geschiebe-Dreikanter oder Pyramidal-Geschiebe. *Jahrb. Kgl. preuss. geol. Landesanstalt. u. Bergakad. Berlin* 1884: 201–210, pl. X, 1885.

[18] Mickwitz, A. von. Ueber Dreikanter in Diluvium von Reval. *Neues Jahrb. f. Mineralogie* **2**: 177–179, 1888.

[19] Reitz, H. Facettengeschiebe aus dem holsteinischen Geschiebemergel. *Ibid.* **2**: 16–20, pls. I–II, 1914. (Many ventifacts were observed on the North German plain by Dr. Frank Leverett in 1908. A personal communication.)

[20] Dücker, Alfred. Die Windkanter des norddeutschen Diluviums in ihren Beziehungen zu periglazialen Erscheinungen und zum Decksand. *Jahrb. preuss. geol. Landesanstalt Berlin* 1933, **54**: 487–530, 1934.

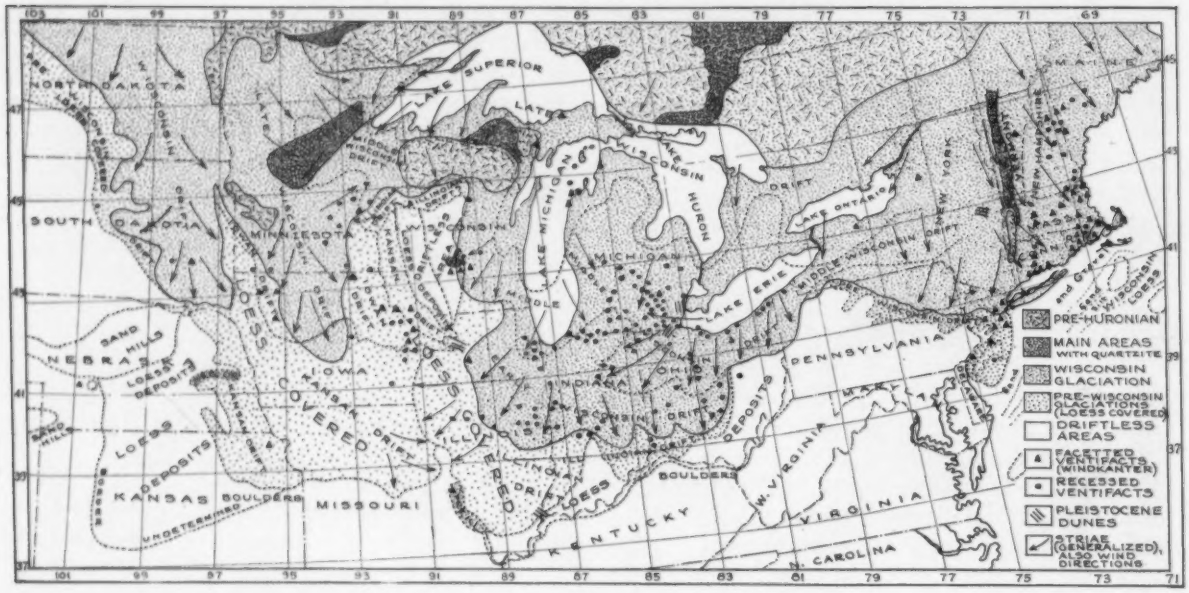
[21] Cailleux, André. Cailloux éoliens et solifluxion en France et en Europe septentrionale. *Soc. géol. France Bull.*, ser. 5, **8**: 719–729, pl. XLIV, 1938.

[22] Bather, F. A. Dreikanter in drift of glacial origin. *Quart. Jour. Geol. Soc. London* **55**: xc–xci, 1899.

—— Wind-worn pebbles in the British Isles. *Proc. Geologists Assoc.* **16**: 396–420, pl. XI, bibliog., 1900.

[23] Jackson, J. Wilfred. The association of facetted pebbles with glacial deposits. *Manchester Lit. and Philos. Soc. Mem. and Proc.* **62**: 1–16, pls. I–II, 1918.

[24] Wills, Leonard J. On the occurrence of wind-worn pebbles in high-level gravels in Worcestershire. *Geol. Mag.*, ser. 5, **7**: 299–302, pl. XXV, 1910.



MAP 1. The work of wind during the Pleistocene glaciation of North America. Boundaries of glacial formations by Frank Leverett.

THE PLEISTOCENE GLACIATION OF NORTH AMERICA—GENERAL

Distribution of Ventifacts within the Glaciated Area of North America

From our knowledge of the existing continental glaciers we are justified in assuming that much the same conditions prevailed in North America during the Pleistocene glaciation, modified only by the different terrane over which its glaciers advanced.[25] Consequently in 1935, after observing the conditions within the periglacial area of the Greenland glacier, I sent out a "call for information" to colleagues, requesting that they report to me localities where ventifacts, whether facetted or ribbed, were known to them,[26] and I echoed this call in 1942.[27] Earlier published material had related almost entirely to facetted ventifacts (*einkanter*, *zweikanter*, or *dreikanter*), that is, facetted, sand-polished pebbles or boulders.[28] The Greenland studies had shown that a contrasted type was likely in the case of glaciated regions to prove more important because produced from rock varieties which are far more widely distributed within glaciated regions, and, furthermore, are far more easily discovered. The facetted ventifact is shaped from rocks which are of a homogeneous, or nearly homogeneous, rather finely crystalline type. By far the larger number of these appear to be of quartzite rocks with a fairly limited distribution within the glaciated regions. The ribbed or recessed type of boulder, such as was found on the outwash area of the Greenland glacier, is by contrast exceptionally non-homogeneous and is most easily discovered when dikes or veins of more resistant material—generally aplitic dikes or veins of quartz—traverse the boulder. The only areas where boulders of this type could be derived would appear to be those where the "fundamental complex" of the Archean, scattered as this is through the pre-Huronian region of Canada and the Northern United States, has been exposed (see map 1).

Over the areas of pre-Cambrian rock the Pleistocene glaciers advanced, and boulders from

[25] Hobbs, W. H. The Pleistocene glaciation of North America viewed in the light of our knowledge of existing continental glaciers. *Bull. Am. Geog. Soc.* **43**: 641–659, 1911.

[26] Hobbs, W. H. A call for information. *Jour. Geology* **43**: 551–552, 1935.

[27] Hobbs, W. H. Wind—the dominant transportation agent within extramarginal zones to continental glaciers. *Jour. Geology* **50** (5): 558, 1942.

[28] The term ventifact proposed by Bryan (*Nat. Research Council, Reprint and Circular Series*, no. 98: 31) seems generally to have been interpreted as restricted to this type, though clearly intended to include all stones which have been given either shapes or surfaces through the action of sand driven by the wind. It is important to distinguish as contrasted types, the *facetted* and the *recessed*.

this source are by the thousand spread far and wide over the United States.[29]

Under the sand bombardment such injected dikes or veins within the boulder increasingly project from the general surface like ribs (see figs. 4–5, 7–11, and 15), and the main mass of the boulder is correspondingly recessed. Areas of quartzite rocks are of relatively limited occurrence. They are associated particularly

FIG. 11. Collection of recessed ventifacts at Ann Arbor, Michigan. (Photo by I. D. Scott.)

with the Huronian formations, and a noteworthy area, but of Cambrian age, is that of the Vermont quartzite formation.

In so far as the recessed boulders have been accorded any attention by glacialists, they appear to have been looked upon as relics of decomposition weathering. None of the boulders that I have seen have been found associated with decomposed material of the same kind upon the ground underneath, and the recessed portions of the block, where decomposition would be presumed to have been most extensive, show as a rule no indication whatever of such weathering, but are hard and unaltered. Moreover, composed of gneiss or of coarse-grained igneous rock, this recessed portion reveals the different degrees of resistance to bombardment of its constituent layers or of its different mineral constituents. Within the Central States, where such drilled boulders are so very numerous, they are sometimes associated with others of the same rock, but these without positive proof of sand-blast action. By analogy with the Greenland occurrences, some of these are believed to have been entombed within the outwash or other protecting deposits and so were not exposed to the sand-blast action. Within this wide area of the Central States, moreover, the rocks in situ are Paleozoic sediments, and so any such extensive decomposition assumed must have taken place before the transportation from Canada by the glacier. It seems likely that the hypothesis of weathering has been offered because studies of glaciation had heretofore supplied no possibility of their origin in sand-blast action.

Geologists personally unfamiliar with desert sandstorms and their effects will find it difficult to appreciate what these storms accomplish in drilling the exposed rocks. The major accomplishments are sharply confined to the first yard or so above the ground, for saltation of the heavier sand grains and pebbles up to an inch or more in diameter is restricted within this air layer. Above this layer sand and dust are carried laterally. This has been proven by many observations made in the Libyan desert.[30]

The short time during which rock and other materials are drilled away is amazing. A tin plate left exposed in a single sandstorm had all the tin removed from the exposed surface. A bottle similarly exposed acquired the surface of ground glass. Iron telegraph poles erected along the railway were polished to the distance of a yard above the ground by the first storms. Granite inselbergs show bright polish within the same limits (fig. 12). The ancient Roman fort of El Deir is undercut by drifting sand (fig. 13). The best gauge of the time required to accomplish a definite amount of erosion is supplied by the corner posts of a cemetery in the Great Oasis of Libya. The material is adobe bricks with a veneer of adobe. On the windward side the veneer was removed by the sand blast to the height of a yard within a few months (a fraction

[29] The laymen have greatly assisted the glacialist in determining the distribution of the recessed ventifacts through making collections of them to set up as "natural curiosities" in rock gardens, driveway entrances, and even as grave markers and monuments in cemeteries. They are also erected as class or other memorials on college campuses. In by far the greater number of instances they appear to have been transported by human agencies for distances of a few miles only.

[30] Hobbs, William H. The erosional and degradational processes of deserts, with especial reference to the origin of desert depressions. *Annals Assoc. Am. Geographers* **7**: 25–60, 9 fig., 13 pl., especially pls. XVII–XXIV, 1917.

—— The peculiar weathering processes of desert regions with illustrations from Egypt and the Soudan. *Michigan Acad. Science, 20th Rept.*: 93–99, 5 pl. 1918.

—— A pilgrimage in northeastern Africa, with studies of desert conditions. *Geog. Rev.* **3** (5): 337–355, 12 fig., 1917.

FIG. 12. An inselberg near Khartoum drilled and polished by the sand blast within a zone about a yard in height near the ground. (Photo by W. H. Hobbs.)

FIG. 13. Fort of El Deir in the Great Oasis of the Libyan desert undercut by the sand blast. (Photo by W. H. Hobbs.)

only of one year), and in the lower levels near the ground the undercutting was measured as 6 inches (fig. 14).

It is within this narrow ground zone of saltation of sand and pebbles that the stranded boulders of the outwash plain of Greenland are included.

In the case of the boulders associated with continental glaciation, the fact that evidences of extensive decomposition weathering are so rare as to be almost if not quite unknown for those found in exposed positions, as well as their uniformly hard and smooth surfaces, lead to the belief that practically all have been modified in shape and are polished by sand blast. The essential rarity also of glacier-facetted and striated boulders (except within till deposits) strongly supports this view. Yet the terrane over which the North American continental glaciers moved must have given boulders of englacial origin with glacial facetting and striation a very wide distribution. This is attested by the unleached clay, the "grist of the glacier mill," which makes up so large a part of the till deposits. The conclusion is inescapable that the edges of the once glacier-facetted and later exposed stones have since been rounded off and their striations drilled away by the sand blast. Observation of many thousand boulders within the glaciated area in North America has forced this conclusion upon the writer.

Facetted and recessed ventifacts are those only which have thus far permitted us to prove the manner of their shaping. Experience within desert areas has shown that such stones—windkanter and stone lattice—are not common there but must be sought out. There are other varieties of ventifact character which are found either alone or with the recessed or facetted types, but they are apparently less common and less well recognized. Most marked of these have grooved, rippled, or pitted surfaces. A locally pitted facetted ventifact from Iceland is shown in figure 6 (p. 371).

Yet it is now clear that all exposed stones within wide areas of desert regions, and of glaciated areas as well, must have been subjected to the same sand-blast action as the more obvious ventifacts which are found there. One must conclude, therefore, that special conditions, either the complexity of constitution in the case of recessed ventifacts, or other initial conditions not yet too clearly understood for the facetted ones, account for their special shaping.

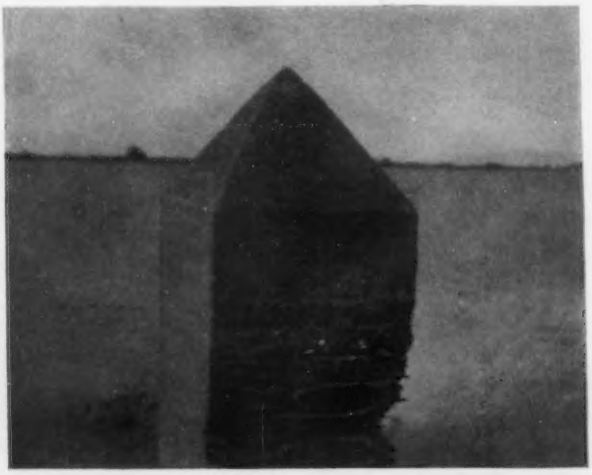


FIG. 14. Work of the sand blast in the Libyan desert within a period of a few months. (Photo by W. H. Hobbs.)

FIG. 15. Recessed ventifact from Bloomfield, Oakland County, Michigan. (Photo by E. T. Boardman.)

Not boulders only, but rocks in place within the glaciated area, when not sheltered from the anticyclonic winds, should similarly, but much less markedly if in elevated positions, reveal the effects of the sand-blast action. This is particularly noteworthy in the case of exposed cliffs.

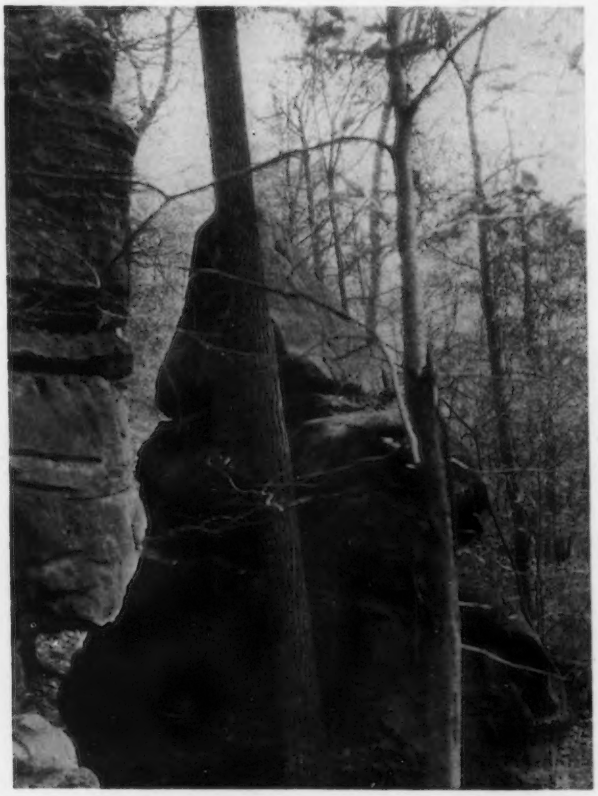


FIG. 16. Sand-blast action displayed by the Sharon conglomerate in cliffs at Hinckley, Ohio. (Photo by A. B. Williams.)

FIG. 17. Cross-bedded structure of the sand layers within the Sharon conglomerate of Hinckley, Ohio. This is brought into relief by sand blast. (Photo by A. B. Williams.)

With rocks unsusceptible to decomposition weathering, such as sandstone, the effect of sand-blast action is to be definitely proven whenever there is a marked internal structure. Cross-bedded sandstones throughout the glaciated region reveal their structure drilled into relief by the sand blast. Photographs of the Sharon conglomerate from Hinckley, near Cleveland, Ohio (figs. 16 and 17), might be duplicated by views I have taken within the Libyan desert.[31]

Map to Show the Work of the Glacial Anticyclone during the Pleistocene Glaciation of North America

The accompanying map (map 1) sets forth the distribution of evidences of the work of the glacial anticyclone during the Pleistocene within the glaciated area of the United States. It has not been extended to the Canadian area. For the boundaries of the deposits for the different glacial invasions I am indebted to Dr. Frank Leverett, to whom my thanks are due for this service and for much valuable information. Though most of the recessed-ventifact localities represented upon the map are from my own observations, a large number are from occurrences already noted in print or contributed to me by colleagues and former students. The arrows upon the map, chiefly within the area of

[31] See also views published by Johannes Walther in *Das Gesetz der Wüstenbildung*, 2nd ed., pp. 155, 177, 193. Leipzig, 1912.

the Wisconsin glaciation, show at the same time both the generalized directions of the ice movement and, approximately, of the strong anticyclonic winds as well. The map also indicates —considerably generalized—the source areas of the two contrasted main types of ventifacts. For the recessed type, it shows the pre-Huronian areas within which enclaves of "fundamental complex" occur, and also an area of injected gneisses in the Berkshire Hills of New England. For the facetted type, the principal quartzite-yielding areas of the Huronian are represented, and also the Cambrian quartzite in northwestern New England. Such ventifacts are also produced from both fine- and medium-grained igneous rocks from pre-Cambrian and other later intrusives, notably in the Adirondacks and New England.

The map shows that ventifacts have been found resting upon all of the drifts. The number of localities entered upon the map clearly affords little indication of actual abundance, but shows rather the areas examined, though the loess deposits over the older drifts must mask occurrences within those areas. The paucity of localities for ventifacts within New York and Pennsylvania is, however, otherwise explained —the rather general absence of boulders in those states east of Erie, Pennsylvania. The glacial striae which indicate the routes of supply from the sources of injected rocks and quartzite, largely explain their absence.

There have been entered upon the map the localities for facetted ventifacts which were collected by Wentworth and Dickey[32] as a result of an extensive questionnaire carried out for the entire United States without any reference to the glaciated area. Of the 109 geologists to whom the questionnaire was sent, 39 replied and reported 61 localities. Seven localities were within the desert region of the southwest. The others were either within or near to the glacial deposits, five of them on the eastern border of the glaciated area of Colorado. The others, 49, have been entered upon the map. That all but the desert localities should be associated with the Pleistocene deposits is of much significance respecting their glacial origin, for at least the Appalachian and the Rocky Mountain regions contain rocks suited to the formation of ventifacts of either type.

The Nature and Distribution of the Loess Which Covers the Pre-Wisconsin Drifts

It has long been recognized that, if we except the deposits connected with low-latitude deserts, all widely distributed loess deposits have been found associated with the areas of former continental glaciation. Though once believed to be of fluviatile origin, the role of the streams in loess distribution is now regarded as mainly secondary —a redistribution of material already deposited by the wind.

Studies of the periglacial area of the Greenland glacier have indicated that loess is being distributed by the storm winds of the glacial anticyclone during the long winter season, using glacio-fluvial material extramarginal to the glacier and laid down during the brief summer season. This loess is therefore contemporaneous with the glacier itself, and since the winds of the anticyclone are everywhere nearly normal to the glacier front, we may assume that likewise in the Pleistocene the loess should have been laid down within and around the extramarginal zone, and largely without reference to present-day wind currents.

There is next the ice front a zone of eolian deflation whose width has not been accurately determined, and within which no eolian deposition takes place but only deflation. It is because of this that pebble pavements are here laid down. As one passes out from the zone of deflation, these pebble pavements disappear as surface deposits but loess takes their place. Still farther out the outwash deposits thin out beneath their cover of loess until they are replaced altogether by the loess deposits (see fig. 18).

As has been shown, the surface deposits of loess within the glaciated area, except where locally exposed by considerable erosion, are peripherally disposed to the Wisconsin Drift and must be assumed to belong in large part at least to the latest or Wisconsin glaciation. The surface deposits have heretofore been described under the names of Iowan and Peorian loess.[33] Loess in Iowa largely overlies the Kansan and Nebraskan drifts. In Europe also the loess distribution is peripheral to the latest (there the

[32] Wentworth, Chester K., and Robert I. Dickey. Ventifact localities in the United States. *Jour. Geology* **43**: 97–104, 1935.

[33, 34] Chamberlin, T. C. Supplementary hypothesis respecting the origin of the loess of the Mississippi Valley. *Jour. Geology* **5**: 796–802, 1897.

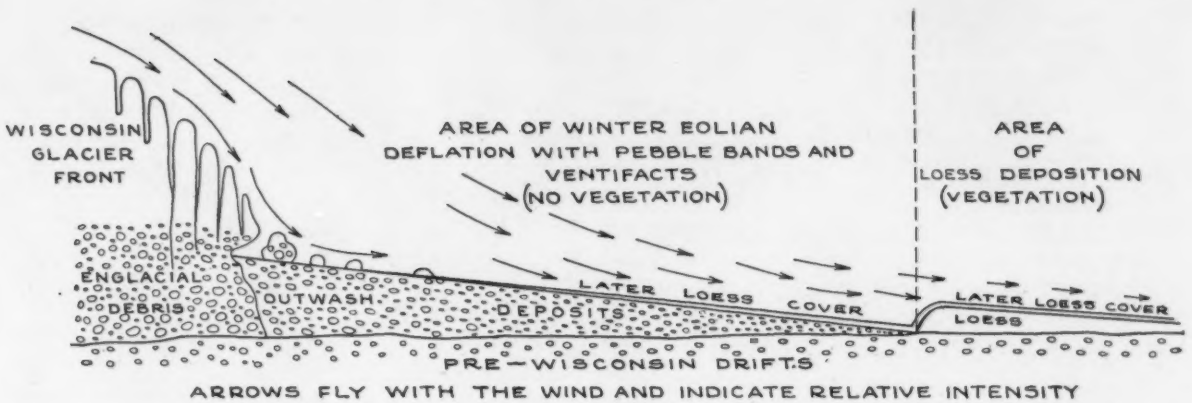
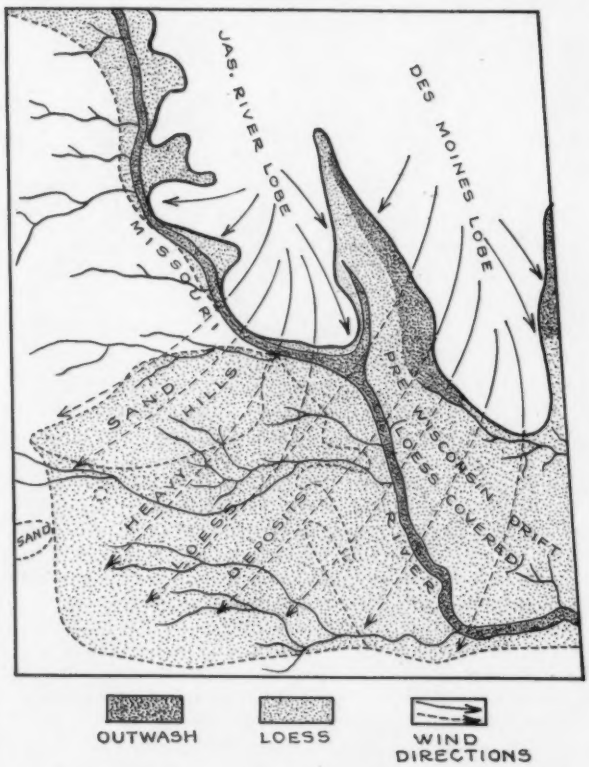

WISCONSIN GLACIER FRONT
AREA OF WINTER EOLIAN DEFLATION WITH PEBBLE BANDS AND VENTIFACTS (NO VEGETATION)
AREA OF LOESS DEPOSITION (VEGETATION)
ENGLACIAL DEBRIS
OUTWASH DEPOSITS
LATER LOESS COVER
LATER LOESS COVER
LOESS
PRE-WISCONSIN DRIFTS
ARROWS FLY WITH THE WIND AND INDICATE RELATIVE INTENSITY

FIG. 18. Diagram to illustrate the laying down of outwash with included pebble and boulder bands, surrounded by a raised loess ridge where vegetation has developed. Later a thinner deposit of loess has formed a veneer over outwash and loess alike. As the glacier front retired, the area of outwash was reduced and vegetation encroached from its borders.

Wurm) glaciation and overlies the earlier drift formations. Though these facts of loess distribution were early recognized, no adequate explanation for them had been offered. As long ago as 1897 T. C. Chamberlin, in a general paper on the origin of the loess read before section E of the American Association for the Advancement of Science, made the facts very clear:[34]



MAP 2. The directions of the winds of the glacial anticyclone over the James River and Des Moines lobes of the Keewatin (late Wisconsin) glaciation. The darker stippled areas are of outwash. A large part of this loess deposit was derived from the broad silt flood plain of the Missouri River.

> The second significant feature is the distribution of the loess along the border of the former ice-sheet at the stage now known as the Iowan. . . . The elaborate paper of McGee made us familiar some years ago with this relationship in eastern Iowa. The studies of Calvin and his colleagues, Bain, Beyer, and Norton, of the Iowa Survey, of Winchell and Upham of the Minnesota Survey, of Todd of the South Dakota Survey, and of Salisbury, Leverett, Udden, Buell, Hershey, and the writer of the United States Survey, have greatly extended the evidence of this relationship. It has recently been much advanced by the Iowa geologists and by Leverett and Hershey in northwestern Illinois. *Next the border of the ice-sheet the loess is thick and typical, but graduates away with increasing distance from the ice border. . . .*[35] On the border next the ice there are developed the formations designated by McGee paha, elongated domes of quasi-drumloidal contours which are mantled by loess. This superficial loess graduates downwards into loess of coarser and coarser texture until it often passes into a nucleus of sand. . . . These pahas seem to be ice border phenomena.

They have since been considered by Leverett[36] to be sand dunes built up by winds coming off the ice. (See, however, pp. 398–399.)

[35] Italics not in the original.

[36] Leverett, Frank. Wind work accompanying or following the Iowan glaciation. *Jour. Geology* **50**: 548–555, 1942.

In a paper written by Calvin[37] just before his death and published posthumously, an explanation of the loess is offered in "*strong winds coming, probably, from the ice fields to the north which lift silt from the outwash plain.*" He wrote:

> Loess deposition took place after the Iowan ice had retreated to a greater or less extent, after an interglacial interval had actually begun. By such retreat extensive mud flats were left, and as these dried before becoming covered with vegetation, strong winds coming, probably, from the ice fields to the north, carried fine sand and dust from the bare surfaces and deposited them beyond the edge of the Iowan area, out upon the old, eroded Kansan. . . . The color, composition, and calcareous content of the Iowan loess are in perfect accord with the hypothesis just expressed; its geographic distribution around the lobed margin of the Iowan area agrees also with the view; the great thickness of this loess at and near its inner margin and its thinning out with increasing distance from the source of supply, corroborate all other lines of evidence; while the great amount of eolian sand associated with it in a narrow belt surrounding the lobes of Iowan drift lends additional support.[38]

Eleven years later Visher,[39] taking definite account of the glacial anticyclone, reached somewhat the same conclusion as to the origin of the loess.

In general the loess extends over most of the pre-Wisconsin drift formations, though considerably redistributed along the principal river valleys. Along the Mississippi and Missouri Valleys trains of silt extend far beyond the other glacial formations. In southern Indiana and Ohio, where the margins of the Wisconsin glaciation approach those of the earlier glaciations, the loess deposits are found to be extended outward into the driftless area as far as the course of the Ohio river.[40]

It is quite probable that these deposits were carried beyond the river for considerable distances. The general absence of loess within the periglacial zone in Pennsylvania may be explained by the absence of outwash. Here also, according to Marbut's soil atlas,[41] the soils are today too thin for the making of soil profiles. Some loess is found in the river deposits of the Susquehanna and the Delaware, according to a personal report of Professor F. G. Merkle, of State College, Pennsylvania.

Loess deposits should clearly have been laid down in the Atlantic Ocean to the south and east of the New England region (see p. 402). The cores recently obtained from bottom deposits on the outer continental shelf, the continental slope, and below to the extreme ocean depths of more than 2,000 fathoms, have revealed silt deposits of late Wisconsin age as shown by the Foraminifera fauna.[42] Associated pollen indicates that these deposits were at least in part wind-transported. Some of these samples were taken as much as 200 miles from the coast.

The driftless area of the Upper Mississippi Valley should have received at least a border deposit of loess, owing to the proximity of the Des Moines glacial lobe on the west and of the Lake Michigan lobe on the east. As early shown by Salisbury[43] and by Weidman,[44] the beds of Peorian loess extend from near the east border of the Des Moines lobe some 60 miles to the Mississippi and beyond into the driftless area for a distance of 10 miles or more, where they thin out and become interleaved with the surface soils. This belt has since been found by Weidman and others[44] to extend eastward from the Mississippi River 10 to 20 miles and "rarely 30–40 miles." Thinner deposits, according to Martin,[45] are found 50–80 miles east of the Mississippi.

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[37] Calvin, Samuel. The Iowan drift. *Jour. Geology* **19**: 601–602, 1911.

[38] This was written in 1910 or early in 1911. Calvin died April 7, 1911. The first published exposition of the glacial anticyclone had been made in June, 1910 (footnote 3). Conditions within the periglacial area were not to be observed for another score of years, after the University of Michigan expeditions had gone to Greenland. Calvin's remarkable explanation here reproduced is therefore seen to be with little doubt due to the suggestion of the glacial anticyclone, supplemented by keen inductive reasoning from his observations in the field.

[39] Visher, S. S. The time of glacial loess accumulation in its relation to the climatic implications of the great loess deposits [etc.]. *Jour. Geology* **30**: 472–479, 1922.

[40] Leverett, Frank, and Frederick W. Sardeson. Quarternary geology of Minnesota and parts of adjacent states. *U. S. Geol. Survey Prof. Paper* 161: 36, 1932.

[41] *Atlas of American agriculture*, pt. 3: *Soils of the United States*.

[42] Phleger, F. B., Jr. Foraminifera of submarine cores from the continental slope, pts. 1 and 2. *Bull. Geol. Soc. America* **50**: 1395–1422, 1939; **53**: 1072–1098, 3 pl., 6 fig., 1942. See also Henry Stetson, *ibid.* **47**: 339–366, 3 pl., maps, 1936.

[43] Salisbury, R. D. (with T. C. Chamberlin). The driftless area of the Upper Mississippi Valley. *U. S. Geol. Survey, Sixth Ann. Rept.*: 278–307, pl. XXVII, 1885.

[44] Weidman, Samuel (assisted by E. B. Hall and F. L. Musback). Reconnaissance soil survey of part of north western Wisconsin. *Wisconsin Geol. and Nat. Hist. Survey Bull.* 23, *Econ. Ser.* 14: 73–78, 1911.

[45] Martin, Lawrence. The physical geography of Wisconsin. *Wisconsin Geol. and Nat. Hist. Survey Bull.* 36, *Educ. Ser.* 4: 123–125, 1916.

Salisbury also found the loess at Camp Douglas, 60 miles east of the river. The subsequent deep dissection of the area must have carried away much of the surface deposits. However, on the eastern margin of the area and on the margin of the Lake Michigan glacier lobe, Salisbury[46] found loess 8 to 10 feet thick on the drift itself and at one near-by locality just west of it.

An area of Peorian loess and near-by contemporaneous sand hills, located in central and eastern Kansas and Nebraska, has especial interest, since it reaches out southwestward beyond the glaciated area for 200 miles.[47] This seems to be related in position as a deposit by winds from the great twin James River and Des Moines glacier lobes of the Wisconsin glaciation, but of silt derived largely from the flood plain of the Missouri, which is outwash from the James River glacial lobe. The loess is here found to have an extreme thickness of 110 feet near the southeastern border[48] and 60–100 feet at the north, though generally of 30 to 40 feet. Profiles indicate that these wide variations are explained in large part by thinning of the loess westward from the Missouri and by the irregularities of the terrane on which the deposit was laid down, and to some extent by later erosion. After the two lobes had retreated northward and the planetary winds had again taken over control here, the Missouri flood plain still continued to receive large summer contributions of outwash silt from the James River lobe. This was now lifted, and instead of being carried westward as before, was now built up east of the river in thick deposits which thinned out eastward.

While the glacial striae show in a very general way the local directions of the strong anticyclonic winds, these are approximate only. Air currents start down over the surface of the glacier along lines of steepest slope, which is the direction also of the striae, but owing to the rotation of the earth they deviate in a clockwise direction. In Greenland this deviation may be as great as 30 degrees of arc, and winds starting from the east down the ice slope reach the western front from the east-southeast. In the Antarctic, but here counterclockwise, the deviation is even greater.

From the James River and Des Moines glacial lobes during the Wisconsin glaciation, there were east-northeasterly winds over the periglacial area to the west-southwest. This is contrary to the prevailing winds of today and also to the present water drainage lines. (See map 2.)

Underlying glacial deposits, which include the Kansan drift and the overlying Loveland loess, would indicate that this area had probably already stood in a similar relationship to lobes of the Kansan glacier.

To the westward of Minnesota the area covered by the Wisconsin drift passes into what is now a semi-arid region, within which the general absence of any but a very thin grass makes the retention of earlier surface deposits of silt very unlikely. Recent dust storms in which dispersal has extended even to the Atlantic have enforced this conclusion. It is therefore of special interest to find in Montana that remnants of eolian beds, up to 30 feet in thickness, rest upon the pre-Wisconsin glacial drift.[49]

Farther east in the Dakotas, remnants of eolian deposits have been found in the Wisconsin periglacial area, though much more sparingly.[50] The distribution of the loess in Iowa and Illinois is discussed in the sequel (p. 396 and map 10).

The Absence of a Cover of Loess from the Wisconsin Drifts

The geological work of the wind during the retreat of a continental glacier is in sharpest

[46] Salisbury, R. D. Loess in the Wisconsin drift formation. *Jour. Geology* **4**: 929–937, 1896.

[47] Lugn, A. L. The Pleistocene geology of Nebraska. *Nebraska Geol. Survey, 2nd Ser., Bull.* 10: 81 et seq., 1935.

Alway, F. J., and others. The loess soils of the Nebraska portion of the transition region. *Soil Sci.* **1** (5): 405–410, 1916.

[48] Frye, John C. Physiographic significance of loess near McPherson, Kansas. *Bull. Am. Assoc. Petroleum Geologists* **23** (8): 1232–1233, 1939.

Lohman, Stanley W., and John C. Frye. Geology and ground water resources of the "Equus Beds" area in south-central Kansas. *Econ. Geology* **35** (7): 839–866, 1940.

Frye, John C., and Claude W. Hibbard. Pliocene and Pleistocene stratigraphy and paleontology of the Meade basin, southwestern Kansas. *State Geol. Survey Kansas Bull.* 38: 389–424, 1941.

—— Stratigraphy and paleontology of a new middle and upper Pliocene formation of south-central Kansas. *Jour. Geology* **49**: 261–278, 1941.

[49] Calhoun, Fred H. H. The Montana lobe of the Keewatin ice sheet. *U. S. Geol. Survey Prof. Paper* 50: 48–49. 1906.

Alden, William C., and Eugene Stebinger. Pre-Wisconsin glacial drift in the region of Glacier National Park. *Bull. Geol. Soc. America* **24**: 546–551, 1913.

Alden, William C. Physiography and glacial geology of eastern Montana and adjacent areas. *U. S. Geol. Survey Prof. Paper* 174 (Peorian (?) stage of deglaciation, p. 93), 1932.

[50] Todd, J. E. A preliminary report on the geology of South Dakota. *South Dakota Geol. Survey Bull.* 1: 122–124, 1895.

—— Eolian loess. *Trans. Kansas Acad. Sci.* **28**: 200–203, 1918.

contrast with what has characterized the advance and the halt at its most advanced position. On the retreat for the first time the glacier builds up a succession of marginal moraines in partly concentric festooned arcs, with ground moraine (till plain) separating them. These intermorainal areas of surface till are shown on Alden's glacial map of southern Wisconsin[51] and on Leverett and Taylor's glacial map of Michigan.[52] Glacial outwash within these areas is restricted to rather definite drainage lines across the till plains, and by reason of their very limited areas they cannot supply enough dust for any considerable deposit of loess.[53] Such sand and silt as are lifted by the wind coming off the ice will moreover, because of the hummocky surface of the nearer moraines, be laid down as local pockets in the kettles of their surface, or as a thin surface layer of sandy loess on the lately abandoned till plains.

Also by reason of the relatively narrow limits of the outwash, flooding by melt-water during the summer season will be both deep and frequent, with ice-block transportation of boulders a marked feature. These boulders, often shifted as they are and turned over and around in each summer season, will be sand-blasted on all surfaces. The number of such boulders already seen within the township of Ann Arbor is in the hundreds, and the map indicates how wide is the distribution within the area of the Wisconsin glaciation.

Postglacial Eastward Migration of the Loess

After the waning of the Wisconsin glaciation and, probably also, during interglacial periods as well, some eastward migration of the Pleistocene loess cover has taken place. As the ice front retreated to the northward, the areas which had surrounded it while under the control of its anticyclone, gradually passed under the domination of the westerly planetary winds. That under their influence the surface layers of the Pleistocene loess have been lifted and carried eastward seems to be indicated in the present loess distribution. Those lobes of the Wisconsin glaciation which are in contact with pre-Wisconsin glaciated areas (James River, Des Moines, and Lake Michigan lobes) show this effect very clearly, for not only has the loess to the westward advanced eastward so as to be deposited over the zone of deflation off their westward fronts, but a thin loess layer (up to 5 feet in thickness) has moved up over the surface of the Wisconsin drift for a distance of a few miles. No such border zone of loess has been found off the eastern fronts. These facts of distribution pretty clearly indicate that the source of this migrated material is not the Great Plains in the semi-arid region to the west, for such dust travels largely within higher air layers and its distribution is a general one. The prairie lands on the contrary supported herds of elephants, bison, deer, and antelope during the milleniums since the end of the Wisconsin glaciation. As these animals roamed over the prairies, they raised low clouds of dust which would migrate progressively in an easterly direction by the prevailing westerly winds and be halted by the rising and rougher surface of the Wisconsin drift. The deposits laid down in the Old World even during historic time, and the effects of traffic on the surface of the loess of China, together give full warrant for this assumption.

Along the rivers silt from their flood plains, because of variation of water level, will be dried at the margins. Dust will thus be lifted and on deposition will be built up as heavier loess deposits on the eastern border and will thin eastward.

The Nature of the Sands of the Periglacial Areas

An independent line of investigation has recently been undertaken by Cailleux to determine the measure of the work of wind in connection with the continental glaciations of both North America and Europe.

It is a well-established fact that sand grains which have been carried by the wind can easily be distinguished from those that have been transported only by water. The former are rounded, show dulled or mat ("frosted") surfaces, and have been reduced in size, whereas the latter are less rounded and have lustrous surfaces.

Cailleux[54] has examined European sands from

[51] *U. S. Geol. Survey Prof. Paper* 106, pl. III, 1918.

[52] *U. S. Geol. Survey Mon.* 53, pl. VII, 1915.

[53] The intermorainal plains of Indiana (Leverett and Taylor, *U. S. Geol. Survey Mon.* 53, pl. VII, 1915) and of Minnesota (Leverett and Sardeson, *U. S. Geol. Survey Prof. Paper* 161, map plates) have somewhat greater widths of intermorainal till. Those of the Des Moines lobe in Iowa are very much wider and call for a special explanation (see p. 395).

[54] Cailleux, André. Les actions éoliennes périglaciares en France. *Soc. géol. France Comptes rendus*, fasc. 5: 63–65, 1937.

—— Les actions éoliennes périglaciares quaternaires en Europe. *Bull. soc. géol. France*, ser. 5, 6, fasc. 9: 495–505, pl. XXXV, 1936.

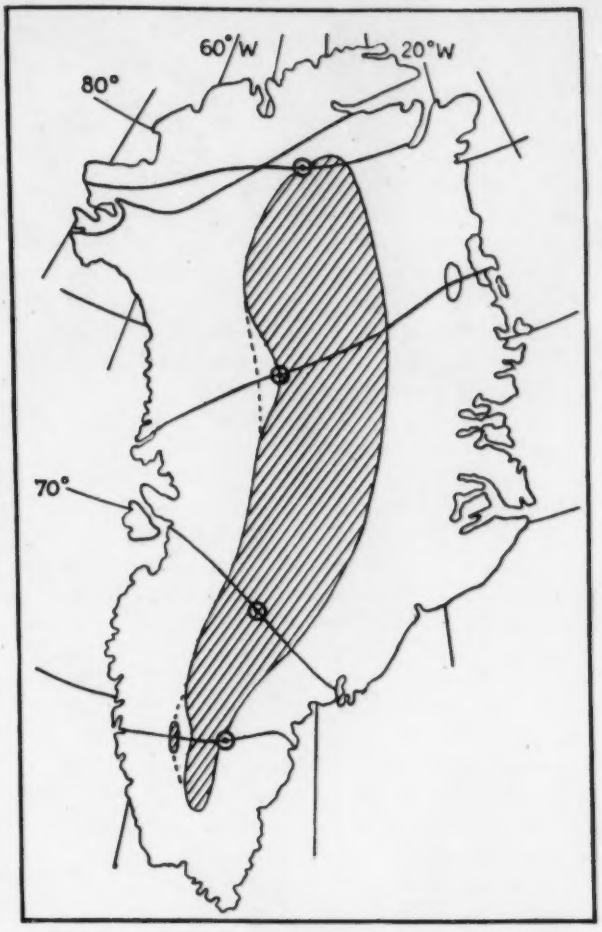
the Quaternary periglacial areas in Poland, France, Saxony, Thuringia, Norway, Sweden, Finland, Holland, Czechoslovakia, Esthonia, and the British Isles. He has found that while dull, rounded sand grains were few or absent from specimens derived from the glaciations of the Alps, or from the smaller ice cap of the British Isles, they were very abundant in those from within a wide border zone of the glaciated area of continental Europe and of North America as well. The conclusion was that these latter sands had been subjected to an intense wind action exceeding in intensity that within tropical deserts. The evidence of wind action on sand grains increased progressively from the center of the glaciated area outward toward their southern margins. Sands transported by storm winds for long distances are many times lifted and deposited. The collisions which bring about the frosted surfaces will therefore be increased in proportion to the distance travelled.

Manner of Nourishment and Enlargement of a Continental Glacier

On the basis of the study of mountain glaciers, which have a forward flowlike movement from their areas of alimentation to their fronts, a like internal movement has been assumed for continental glaciers. Lacking the steeply inclined bed and without a large forward-directed surface gradient, the continental glacier is, except within its frontal zone, incapable of such flow. This I pointed out shortly after the glacial anticyclone had first been described in 1911.[55] The Labradorean glacier in early Wisconsin time extended 1,300 miles from the Labrador center to its front in Ohio. It has generally been assumed to have had a thickness at its center of perhaps 10,000 feet. Its profile, with horizontal and vertical scales the same, would be represented by a thin line drawn by a pen and 6 inches long.

The area of alimentation of a continental glacier is located within its central area, a boss of the domed surface, and distribution is accomplished by the winds of the glacial anticyclone. The only continental glacier which has been studied with sufficient thoroughness to serve as a model is that of Greenland. Sledge journeys of explorers have supplied sections across the areas both of alimentation and of distribution (see map 3).

[55] The Pleistocene glaciation of North America viewed in the light of our knowledge of existing continental glaciers. *Bull. Am. Geog. Soc.* **43**: 655–656, fig. 7, 1911.



MAP 3. Map of Greenland to show the area of alimentation (shaded), the tracks of explorers, and the divides. (After Koch and Wegener.)

A central area of alimentation is one of calms and of relatively light shifting winds. It is also characterized by subzero air temperatures. Even in midsummer the air temperatures are −30° C. and lower. The area is also characterized by high humidity, despite its low temperature, and by almost constant precipitation which goes on close to the surface of the glacier. This snow is powdery and dry and is accompanied by rime. At the borders of this area of alimentation, the air temperatures abruptly rise by as much as 10° C. (see fig. 19).

The distribution of the snow from the central area of alimentation is made by the centrifugal broom of the glacial anticyclone. The winds move everywhere down-slope but deviated clockwise as a consequence of earth rotation. As shown by J. P. Koch, the annual surface

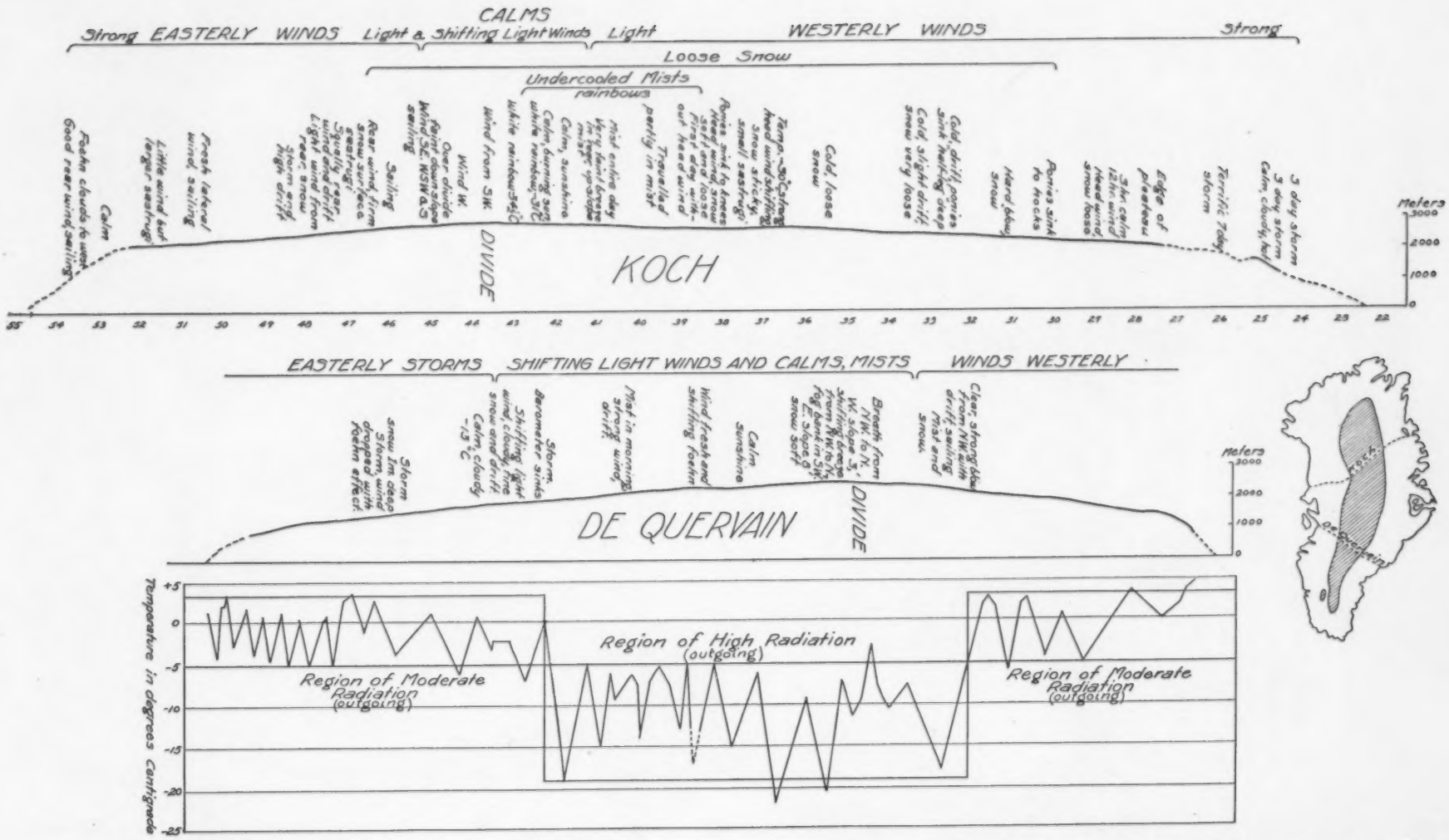


FIG. 19. Transection profiles of the continental glacier of Greenland by J. P. Koch and by A. de Quervain, both made in 1912–13. The diagram at the bottom records successive daily midday and midnight air temperatures during the De Quervain transection. (From *The Glacial Anticyclones*, 1926.)

deposit of snow is thicker as the margin of the glacier is approached, and always during the winter heavy deposits are piled up at the margin.[56] Schematically this is illustrated in figure 20. The vast quantities of snow carried

FIG. 20. Schematic representation of the operation of the glacial anticyclone in distributing snow that is precipitated within the central area of alimentation. (After Hobbs, 1911.)

out by this process have been emphasized by all explorers with experience on either the Greenland or the Antarctic glaciers. Peary wrote in 1898:[57]

> There is one thing of special interest to the glacialist—the transportation of snow on the ice-cap by the wind. No one who has not been there can have any conception of its magnitude. The wind is always blowing, and blowing always on lines which would be gravity lines from the interior. . . . I have walked for days in an incessant sibilant drift of flying snow, rising to the height of the knees, sometimes to the height of the head. If the wind becomes a gale, the air will be thick with the blinding drift to the height of 100 feet or more. I have seen in the autumn storms in this region, round an amphitheatre of some 15 miles, snow pouring down in a way that reminds one of Niagara. When it is remembered that this flow of the atmosphere from the cold heights of the interior ice-cap to the lower land of the coast is going on throughout the year with greater or less intensity, and that a fine sheet of snow is being thus carried beyond the ice-cap to the ice-free land at every foot of the periphery of the ice-cap, it will perhaps be seen that the above assumption is not excessive.

The best picture of these conditions has been supplied by Mawson, whose base in Adelie Land from 1911 to 1914 was at the edge of the Antarctic glacier:[58]

> We led a strenuous existence at winter quarters, buffeting with a sea of drifting snow which poured fluid-thick over the landscape. . . . For months the drifting snow never ceased, and intervals of many days together passed when it was impossible to see one's hand held at arm's length. . . . Such weather lasted almost nine months of the year.

If one takes account of the fact that at every part of the glacier margin the same snow movement is taking place, he cannot fail to appreciate the stupendous measure of this movement and the seemingly inexhaustible supply within the central area of alimentation.

In the Antarctic, where the glacier front in most places reaches to the sea, this vast quantity of cold snow is loaded onto the sea and produces the wide girdle of solid floe which hems in the continent to such an extent that on most coasts it can be reached only by plane.

In Northeast Greenland the snow about the margin accumulates to form a "fringing glacier." In lower latitudes on the east coast the snow goes out to sea, as it does on the north coast, and the girdle of sea ice lies outside, much as it does in the Antarctic. In Western Greenland the snow brought out to the margin during the winter is during the succeeding summer melted, and in addition much underlying ice as well, for we live in a receding hemicycle of glaciation in which glaciers are being diminished rather than enlarged.

Internal flow goes on within the marginal portion of a continental glacier for a distance of between 30 and 50 miles, but gradually comes to an end because of the ever-diminishing gradient of the ice surface. This zone of flow is marked by crevassing, always the indication of internal movement. The direction of movement is always outward, and at the bottom there is quarrying and abrading of the bed and abrasion of the embedded rock fragments, which latter are shaped with facets on which there are striations. These facetted boulders become involved in the lower glacial layers together with boulder clay, which is the product of the abrasion. Inasmuch as the marginal zone of the glacier has advanced from the center of alimentation, all parts of the bed have at some time been subjected to this action, and erratics have been transported in interrupted journeys for very long distances.

THE PLEISTOCENE GLACIATION OF NORTH AMERICA—THE FRONTAL AREA

The Form of the Frontal Lobes

The Pleistocene continental glacier of North America had in the central and western sections

[56] Koch, J. P. Unsere Durchquerung Grönlands 1912–13. *Zeitschr. Gesell. Erdkunde Berlin* 1914 (1): 34–54.
Koch, J. P., and A. Wegener. Wissenschaftliche Ergebnisse der dänishen Expedition nach Dronning Louises-Land. *Meddelelser om Grönland* **75**: 371–382, 1930.

[57] *Geog. Jour.* **11**: 234, 1898.

[58] *Geog. Jour.* **44**: 269, 1914.

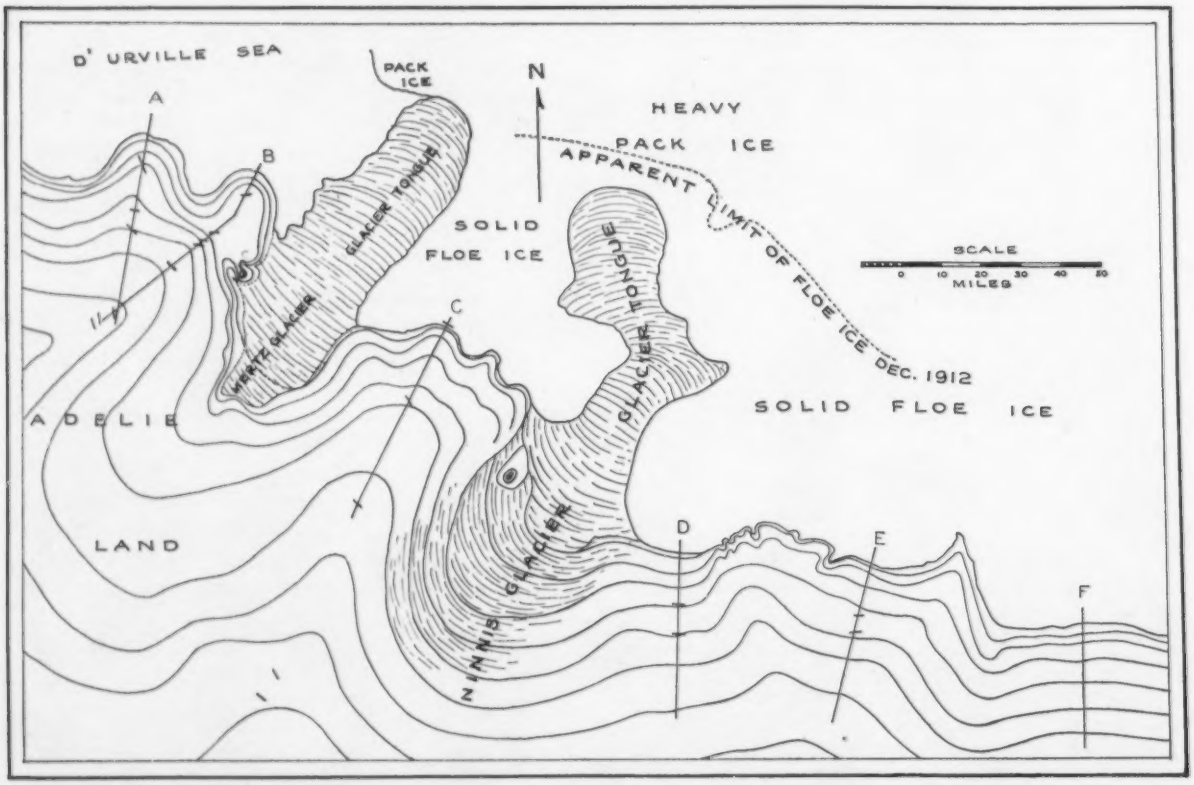
of its southern margin a front diversified by bulging extensions described as lobes. Existing glaciers supply no parallel from areas which have been studied, for the reason that the Antarctic glacier has no periglacial area, and both glaciers have their ice to a large extent contained behind ramparts of mountains with outlet-glaciers issuing only through passes. The Greenland north coast shows somewhat more free marginal movement, but with the underlying and the surrounding terranes so accented that the form of the glacier extensions is largely determined by these irregularities.

In one area of the Antarctic, Adelie Land, though the glacier comes down to the coast and there are evidences that the rock surface beneath has very considerable irregularities, there is yet some approach to local lobate outline and corresponding surface form (map 4). Though less contained than the Greenland glacier or the Antarctic glacier in South Victoria Land, the underlying terrane has here played a large role, as is indicated by the Ninnis and Mertz glacier outlets close at hand, as well as by the small but scattered nunataks. Even the simulated lobe near the base at Cape Denison is seen, by a recently published map, to have projecting *roches moutonnées* along its front.[59]

Profiles of the western marginal portions of the Greenland glacier at the only section where accurate surveys have been made are shown in figure 21 (*A′* and *B′*). These sections may be regarded as typical of a glacier front behind a rampart of mountains. Of such a front we have an example from Pleistocene glaciers in the New York - New England area, and this appears to correspond more generally with prevalent conceptions as illustrated by published work. Profiles from Adelie Land made where the front is nearly straight are given in profiles *D*, *E*, and *F* of figure 21. In profile *B* of the front where it most closely approaches a lobe, the dotted profile is that of *B′* above for purposes of comparison.

Though these profiles show that the fronts of lobes are less steep and the glacier surface at the rear rises far more gradually, the lobes of the

[59] Mawson, Douglas. Geographical narrative and cartography. *Australasian Antarctic Exped. 1911–1914, Sci. Repts.*, ser. A, 1, map opp. p. 8, 1942.



MAP 4. The Antarctic glacier in Adelie Land, showing local lobate extensions. (After Mawson.)

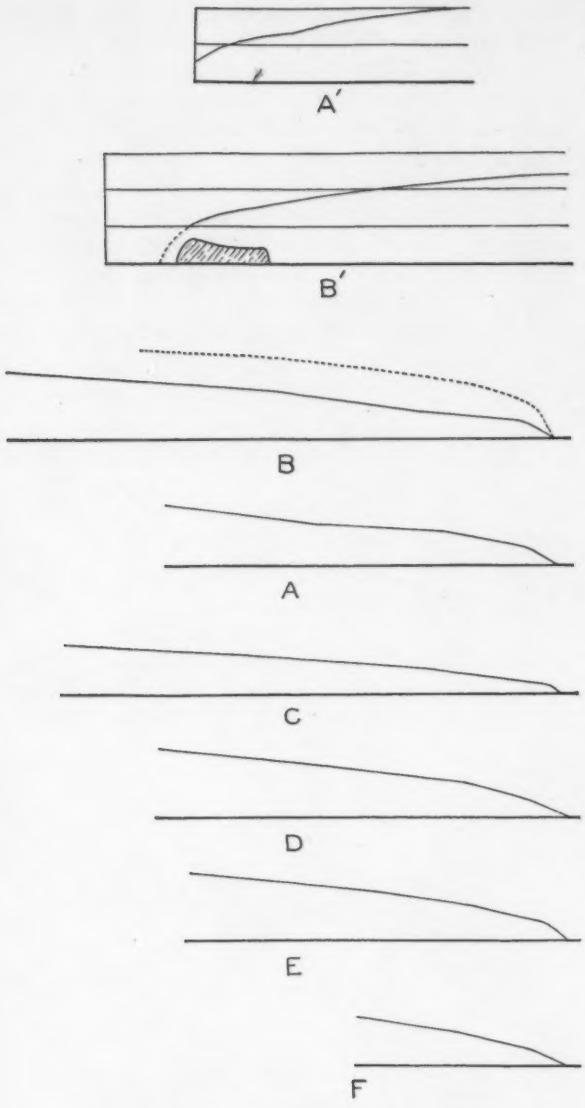


FIG. 21. Profiles across the fronts of existing glaciers. *A′* and *B′* in West Greenland near latitude 71° where the glacier is behind a rampart of mountains (after Wegener Expedition). *D–F* in Adelie Land where the front is nearly rectilinear. *A–C* in Adelie Land where the front is imperfectly lobate. The lines crossing the sections are sledge routes which afford elevations. In all profiles the proportion of the vertical to the horizontal scale is 20 to 1.

Pleistocene glacier in the Upper Mississippi Valley, where there was no containment by the bed, must have possessed fronts even less steep and have been also much thinner.

From studies of our Wisconsin glaciation we know that the lobes were determined in position by shallow troughs, generally either those of mature river basins or else troughs left on the surface of earlier glacial deposits. Lobes are within the marginal zone of glacier flow and therefore assume forms determined largely by the laws of flow of thick viscous fluids, such as molasses. To an approximation the distribution of forces may be studied as though within the horizontal plane. Both lines of flow and those of wind directions which distribute surface snow, are where they meet the lobe margin nearly perpendicular to it (fig. 22*A*). They do not, however, radiate from a center, in which case the outline would be a semicircle (fig. 22*B*); but the lines of flow farther back are also nearly perpendicular to a cross-section. Were these forces the same for equal units of the cross-section, the outline would be a parabola (fig. 22*D*). The actual outline seems therefore to lie between these two types of regular curve (fig. 22*C*). Study of the curves of marginal moraines showed that this is approximately true and that the only reentrants in the glacier front are the cusps separating lobes.

The lines of distribution of the snow by the glacial anticyclone deviate from the lines of flow in a clockwise manner and therefore the modelling of the surface by the anticyclone should tend to produce lobes with the eastern side the straighter. The Des Moines and the James River lobes, which alone reveal both sides for any considerable

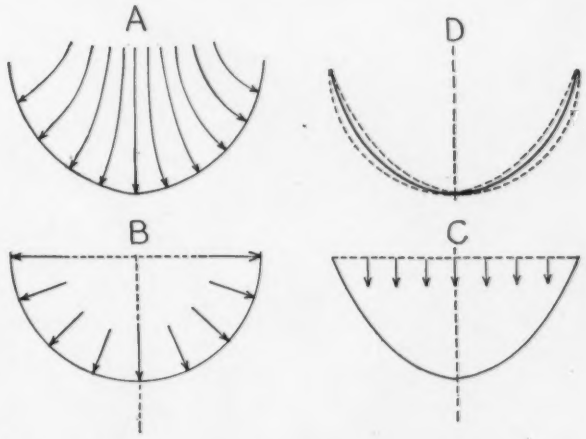
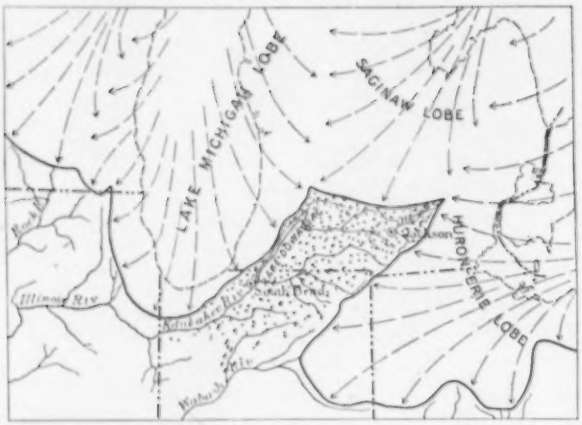
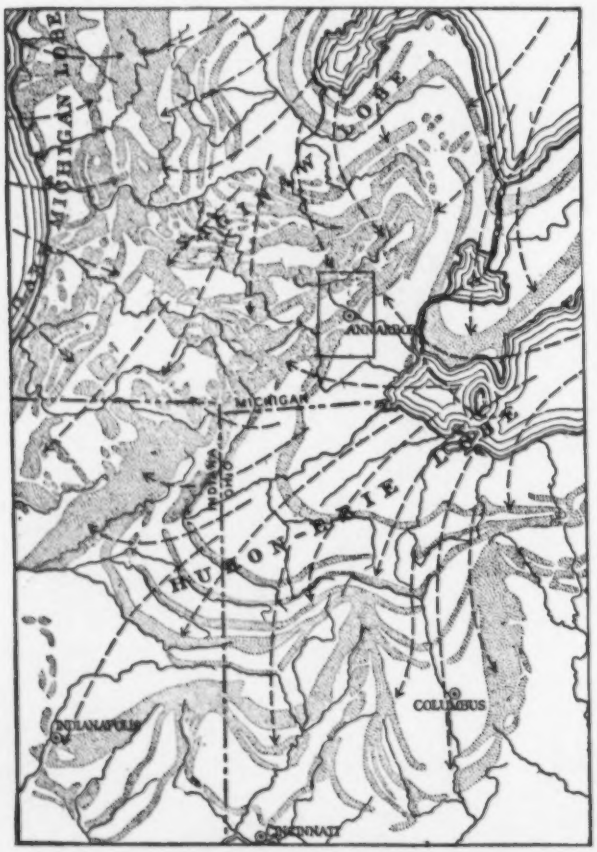


FIG. 22. Diagrams to illustrate the approximate outline of glacial lobes. *A*. Distribution of flow lines within a lobe. *B*. Form of the lobe (semicircle) if the forces were all radial from a center. *C*. Form (parabola) if the forces were all parallel to the axis of the lobe and were equal for all equal units. *D*. The approximate outline between the circle and the parabola.



MAP 5. Huron-Erie lobe after topping the divide. Shows outwash in reentrant area.



MAP 6. The Huron-Erie lobe of the Wisconsin glaciation, which first moved *up* a trough in a southwesterly direction, topped the divide between a former St. Lawrence and Mississippi drainage, and then divided into three smaller lobes directed *down* the troughs of the Scioto, Miami, and White Basins.

distances, seem to indicate that this is true (see map 2, p. 379).[60]

An interesting case where a lobe advancing up a trough has topped the divide and found three subordinate troughs on the other slope, is furnished by the Huron-Erie lobe of the Wisconsin glaciation. The left flank of the lobe has divided into three subordinate lobes which occupied what are today the Scioto, Miami, and White River Valleys (see maps 5 and 6).

The Drainage Extramarginal to the Lobate Areas

There are two main classes of drainage extramarginal to the lobes, according as the trough which is occupied has its axis inclined with the direction of advance or against it—whether the glacier advanced down a valley or up it. In the former case there will be border drainage from both sides toward the front of the lobe, where the two branches will unite in a river which takes its further course along the extended axis of the trough (case I in fig. 23). In case the lobe advances up a valley, drainage is also along the borders but the flow is directed backward and there are two separate streams (II in fig. 23).

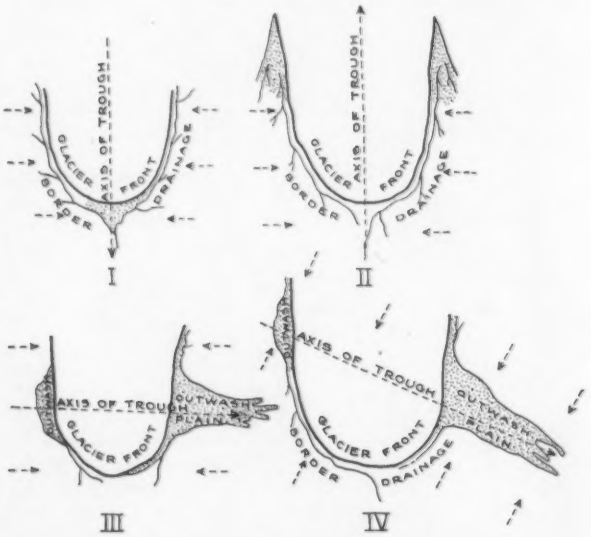


FIG. 23. Diagrams to illustrate the different cases of drainage extramarginal to a lobe. I. When the lobe advances down a shallow trough. II. When it advances up a trough. III. When it pushes at right angles across a secondary trough. IV. When it cuts diagonally across a secondary trough.

[60] Exceptions to the regularity in the lobate front will be noted below in places where dissolution of the lobe has been exceptionally rapid, as was true at the end of the Wisconsin glaciation.

These streams have no outlets but flow into the cusps between the lobes, which are therefore deeply flooded on summer days. Thus are laid down deep deposits of sand and gravel, the so-called "interlobate moraines," which, as respects both their topographic expression and their material, are not moraines but outwash. They are in fact the principal outwash deposits of the glaciated areas during the advancing hemicycle and a principal source of the loess which covers the pre-Wisconsin glacial deposits (see map 5). The other principal sources of loess are the so-called "Iowan drift" soon to be described, the broad flood plains of the glacial rivers flowing from the lobes, and outwash from the expiring Labradorean glacier in New England (see p. 401).

A typical example of the lobe advancing down a trough is the James River lobe of the Keewatin glacier, with the Missouri River and its tributary, the Big Sioux, uniting near the site of Sioux City (case *A* of fig. 24). Lobes advancing up troughs are illustrated by most of the lobes north of the St. Lawrence - Mississippi divide, and especially well by the Huron-Erie lobe (fig. 24*B*), though this advanced over the divide, so that in its later stage the drainage directions (Wabash River) represent case I where the lobe advances down a valley.

As the lobe advanced up the trough, the drainage along its border had the ice for one bank and the ground for the other. The streams thus migrated laterally forward as the ice advanced, and when it halted at its most advanced position, the stream entrenched itself, and its valley became an inheritance for the post-glacial period. The penultimate stage in the Huron-Erie lobe is typical of case II, and the St. Joseph and St. Mary's Rivers today enter the Maumee "backbanded." Such lobes also have episodes of frontal glacial lakes in the receding hemicycle.

Examples of case III are supplied by outwash plains in pre-Illinoian troughs directed east-west on the east side of the Scioto lobe of the Wisconsin glacier in Ohio (map 6, p. 388, and map 11, p. 400), which have been described by Leverett (*Am. Jour. Sci.* **247**: 834–839, fig. A, 1939). An example of case IV will be described below (*C* in fig. 24).

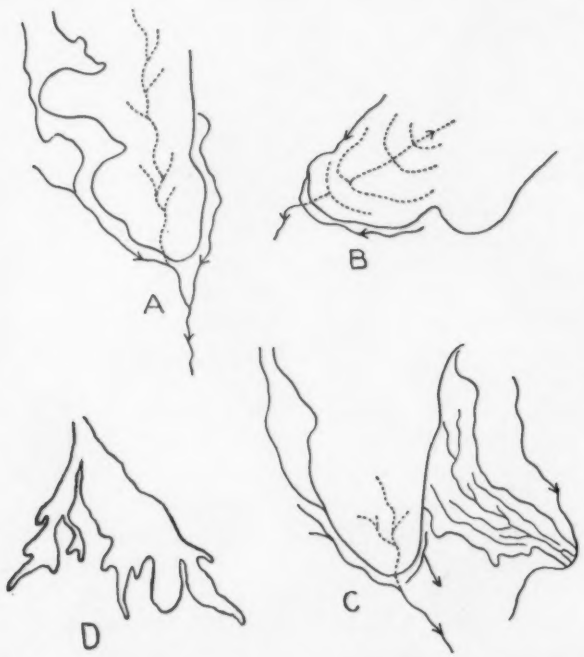


FIG. 24. Examples of extramarginal drainage illustrating the cases in figure 23. *A*. The James River lobe of the Keewatin glacier. *B*. The Huron-Erie lobe of the Labradorean glacier. *C*. Outwash from the Des Moines lobe of the Keewatin glacier. *D*. Outline of flood deposits of the great flood of 1930 from Ford Canyon on the Wasatch foothill slope near Farmington, Utah (from an air photograph).

THE PLEISTOCENE GLACIATION OF NORTH AMERICA—THE RECEDING HEMICYCLE

The Retreat of the Front

For the receding hemicycle we may draw illustrations in fuller measure from the existing continental glaciers, since we are living in a late stage of the receding hemicycle in the Wisconsin glaciation. Though the glaciers have disappeared from North America and Europe, and have withdrawn from their most advanced positions in the polar regions, the evidence of their continued wasting and withdrawal is clearly to be seen. Further evidence that we have not passed out of the latest of glacial periods is supplied by the climatic zones which now characterize our planet. Relative uniformity of temperatures, subtropical in character, accompanied by high humidity, have in all except glacial periods characterized the whole world, including what are now the polar regions.[61]

[61] Lyell, Charles. *Principles of geology*, 11th ed., p. 231, 1872.

Saporta, Gaston von. *Die Pflanzenwelt vor dem Erscheinen des Menschen* (trans. by Vogt from the French ed. of 1879), 397 pp., 13 pl., 118 fig., 1881.

White, David, and F. H. Knowlton. Evidences of

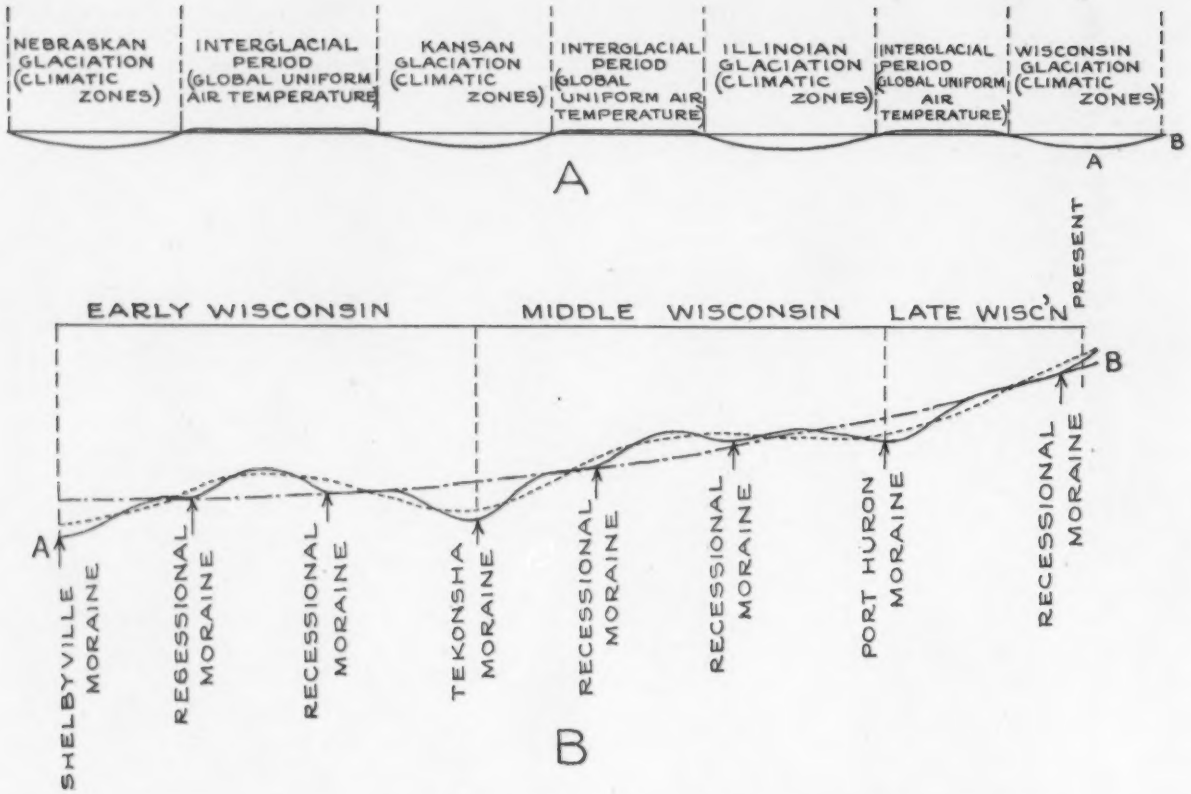


FIG. 25. *A*. Diagram to show the probable variations in solar radiation throughout the Pleistocene Age. *B*. The receding hemicycle of the Wisconsin glaciation, to show climatic alternations. The major moraines and the intermediate recessional moraines correspond each to lowerings in solar radiation.

We may represent the four successive refrigerations of our planet which brought about the Pleistocene glaciations by a diagram in which the lowering of the solar radiation in each period comes on gradually, reaches a minimum, and as gradually returns to normal. The first or Nebraskan glaciation was followed by a normal period—the first interglacial period—characterized by nearly uniform air temperatures. This was followed by the Kansan, Illinoian, and Wisconsin glaciations with their interglacial intervals (fig. 25*A*).

A study of Pleistocene glaciations has clearly indicated that these four periods of reduced solar radiation are themselves characterized by alternations of higher and lower radiation but of smaller orders of magnitude. This is schematically represented in figure 25*B* for the receding hemicycle of the Wisconsin glaciation up to the present time. Units of the lowest order of magnitude, as has been shown by study of mountain glaciers, may be as short as a fraction of a century.

These changes are registered in the varying degrees of dominance of the glacial anticyclone over the planetary system of the winds. Stronger during the winter, in the summer the anticyclone is invaded at its margin by the planetary winds for distances of tens of miles. These winds are in Greenland always light and moist and very often bring warm rains. As a consequence, within a marginal zone of the glacier not only are the snow accumulations of the preceding winter melted, but the surface layers of glacier ice as well. This zone of thaw extends from the margin in to the so-called névé line, where the surface layers of snow laid down during the last winter remain unmelted throughout the succeeding summer (see fig. 26).

paleobotany as to geological climate. *Science* **31**: 760, 1910.

Knowlton, F. H. Evolution of geological climates. *Bull. Geol. Soc. America* **30**: 499–566, 1919.

Hobbs, W. H. Climatic zones and periods of glaciation. *Bull. Geol. Soc. America* **40**: 735–744, 1929.

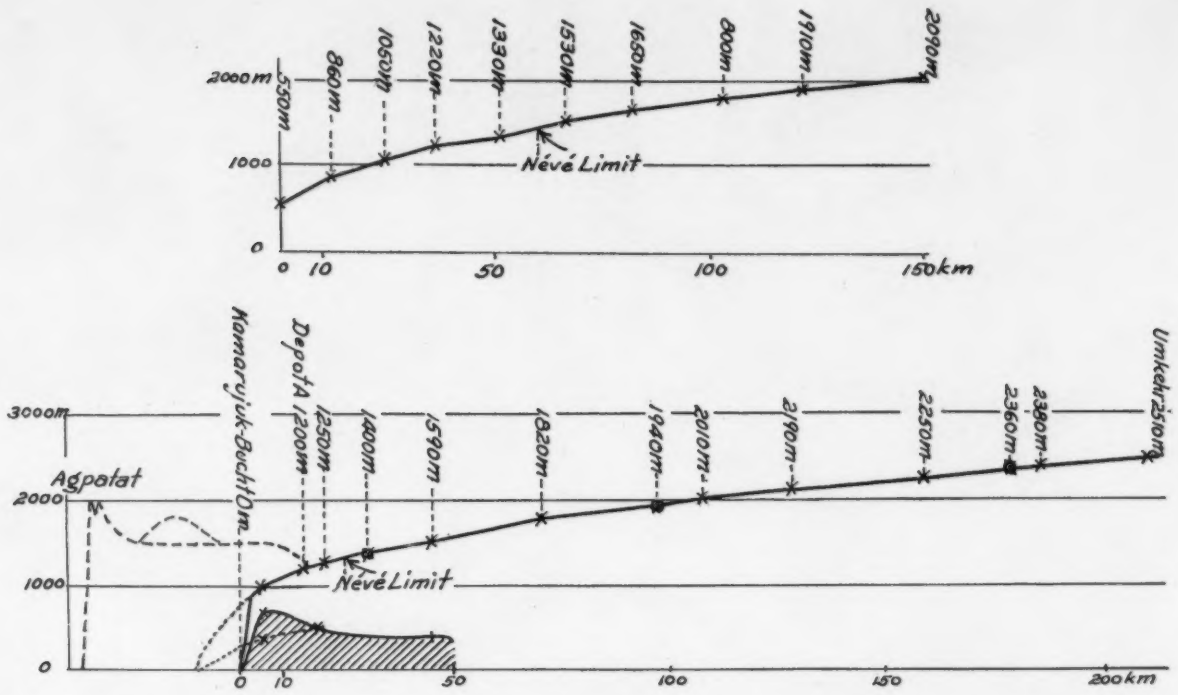


FIG. 26. Profiles across the western margins of the Greenland glacier near latitude 71°. The névé line (*Firngrenze*) is here from 20 to 60 kilometers from the margin. (After the Wegener Expedition.)

On the flatter lobes of the Pleistocene glaciers the névé line under the same climatic conditions would be carried much farther in from the margin. Since the study of icebergs was made in the southern seas by the Challenger Expedition, it has been known that glacier ice is melted but little by the warmer air when the bergs arrive in lower latitudes, but almost entirely by the rains. Glacier lobes will therefore be reduced, not by any considerable recession of their margins, as has been so generally assumed on the basis of study of mountain glaciers, but by a melting of their upper surfaces which results in a progressive thinning of the lobe. With nutrition now cut off for the ice outside the névé line, motion near the front ceases and the outer section of a lobe becomes inert or dead, and the névé line continues to recede until a further drop in the amount of incoming solar radiation gives renewed vigor to the glacial anticyclone. It then begins to build up a new front at the rear of the névé line and pushes this line back some distance in the direction of the glacier margin. This forms a new front of the active glacier, internal movement is set up behind it, and a new recessional moraine comes into existence.

The picture presented here is of a glacier front with an extended plateau of dead ice[62] outside, which may extend as far out as the last preceding recessional moraine. This dead forward extension of the still active glacier may remain unmelted for centuries, but eventually it disappears, leaving behind a plain of till or ground moraine (see fig. 27). After the ice surface has descended into the bottom layers with their englacial rock materials, a veneer of bouldery clay will permit forest vegetation to develop. This insulating veneer will further retard final dissolution.

In its later stages before final dissolution, the dead sheet of ice outside the new active front will be cut through by surface drainage lines and thus separated into broad ice slabs. These slabs with included englacial debris may, during the summer days, be lifted by the flood waters and

[62] The term "stagnant ice" has come into use for ice that is inactive, but "dead" seems to me a far better term. The term stagnant applies especially to water which is without flow and also foul, and continental glaciers are without flow except at their fronts. "Stagnant" is, moreover, so far as I know, never used except for nonviscous fluids. This ice is dead, both because it has lost all activity permanently and because the process of dissolution has begun.

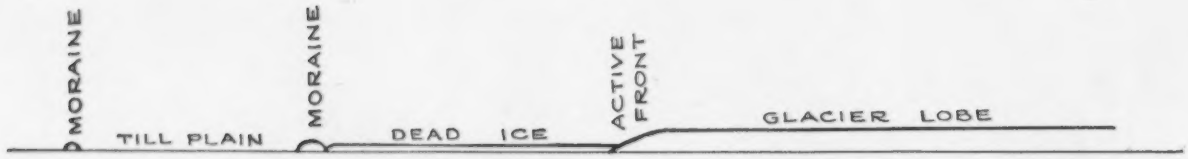


FIG. 27. Schematic profile across the front of a glacier lobe during the receding hemicycle of glaciation.

in interrupted journeys travel in the outwash channels, perhaps for very long distances. The only example of dead glacier ice known to me today is supplied by the detached masses south of McMurdo Sound in South Victoria Land, Antarctica. These were first described by Ferrar as "ice slabs," [63] but were later surveyed by Taylor.[64]

The Spacing of Recessional Moraines

The distances separating moraines within a recessional series give us a measure of the reconquest of the glacial anticyclone by the winds of the planetary system. The dominance of the anticyclone is greatest at the culmination of the period corresponding to the maximum glacier advance, but it also depends upon the latitude, being least in the lowest latitudes attained, other things being equal. The shorter the intermorainal distance, the greater the dominance of the anticyclone, and the greater the distance, the more potent is the summer attack of the rains.

Since the rains are brought by low-pressure areas coming from the west-southwest, the effective attacks must necessarily be made upon the west side of the glacier. In Greenland it is on the west side that the rains of the planetary system of winds have reconquered from the glacier a strip of the land 100 miles in width; while on much of the east and north coasts the anticyclone is still unloading its burden of snow upon the sea. This main attack from the west was the case also with both the Labradorean and Keewatin glaciers of the Pleistocene, as is shown by the large map of the area (map 1, p. 374) as well as by maps 7 and 8, pp. 393–394. The general map shows only the three major moraines, the Shelbyville, Tekonsha, and Port Huron, which border and separate the three divisions of the Wisconsin glaciation. Though these are separated in the west so that the width of the early Wisconsin is 100 miles or more, and that of the middle Wisconsin more than 50 miles, the three moraines in western New York are crowded together within a space of 30 miles. The recessional moraines also, as shown by the map 7, are widely separated in the west.

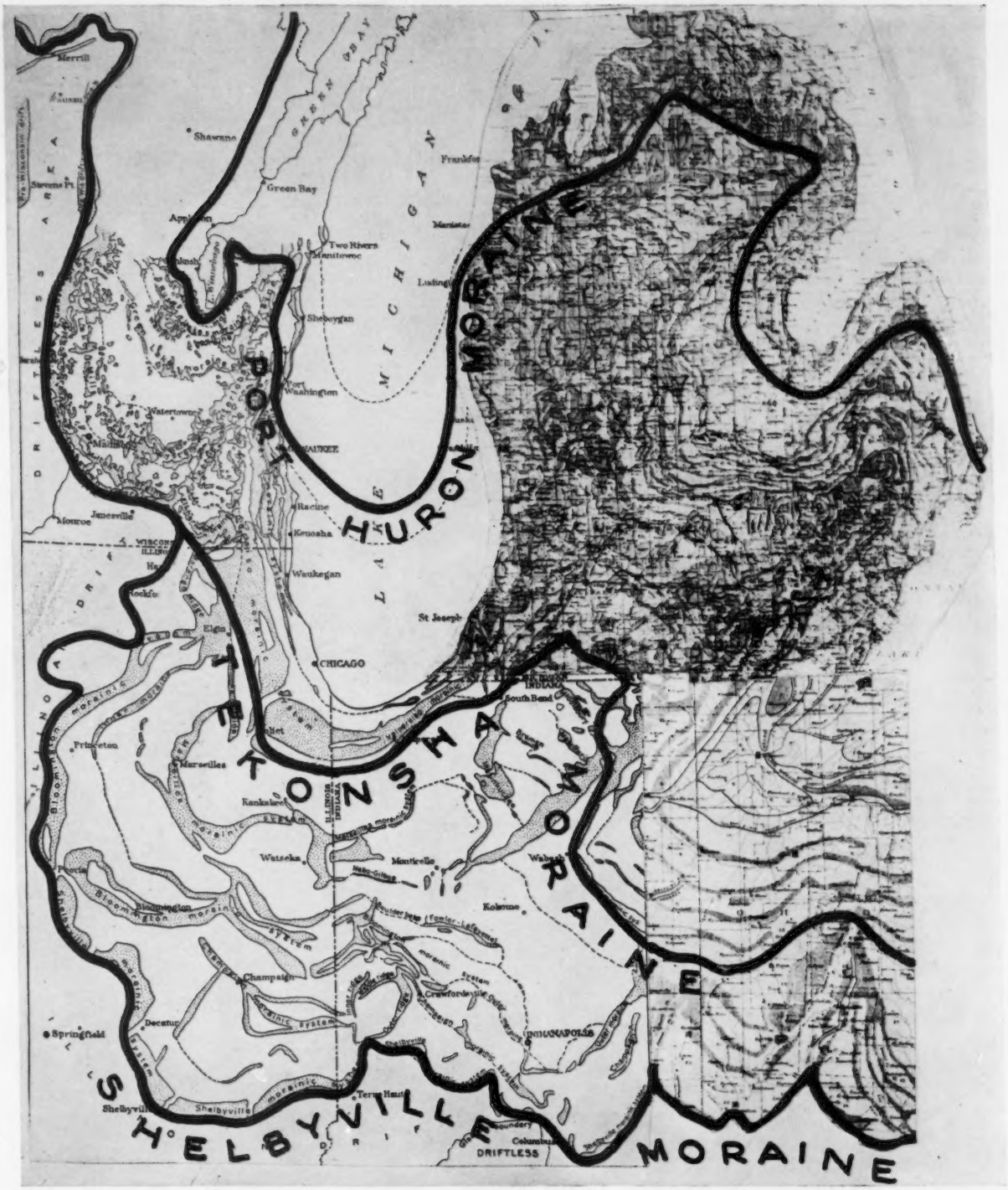
If studied in a direction from south to north, the intermorainal spaces reveal something of the relative effect of winter vigor of the anticyclone and of summer invasion by the rains. The former should be at a maximum and should fall off from the stage of maximum glacier advance, but it should be relatively powerless to aliment the glacier in the waning stages of the late Wisconsin. The invasion of the rains should exert their maximum effects in the southern latitudes, but even in the highest latitudes, by reason of the dying stage of the anticyclone, their effect would be pronounced. The net results of these opposing influences appear to be revealed in the intermorainal spacing. The glacial anticyclone has clearly dominated in the middle Wisconsin for the latitude of southern Wisconsin and southern Michigan (41°30′ to 43°30′), where the moraines are a few miles only apart; and the planetary wind system for both the early Wisconsin in the latitude of southern Illinois (38° to 41°) and the late Wisconsin north of 45°. (See map 7, p. 393.)

The Keewatin glacier had a phenomenally rapid growth during late Wisconsin time. This glacier advanced from its center in Canada in a direction south all the way to south central Iowa near latitude 41°; or through no less than nine degrees of latitude (about 650 miles). Its retreat was remarkable, especially at the south where the effect of waning vigor in the anticyclone was added to that of the southern rains. The retirement of the outermost front of the Des Moines lobe to its halt at the first recessional moraine (Mineral Ridge) was no less than 50 miles, and the next retirement was of 75 miles (see map 9, p. 395). The James River lobe, which

[63] Ferrar, H. T. *Nat. Antarctic Exped. 1901–1904, Nat. Hist.* 1, *Geology:* 64, 73, map in pocket, 1907.

[64] Taylor, Griffith. In: *Scott's last expedition* 2: folded map opp. p. 198, 1913.

—— *Brit. Antarctic (Terra Nova) Exped. 1910–1913:* The physiography of the McMurdo Sound and Granite Harbour region, pl. IV in pocket.



MAP 7. The moraines of the Wisconsin glaciation for the Labradorean glacier (combined from maps of Leverett, Leverett and Taylor, and Alden and Weidman). The courses of the three major moraines were drawn by Frank Leverett.

FIG. 28. Characteristic topography of the loess rim to the "Iowan." Near North Liberty, Johnson County, Iowa. (Photo by W. H. Hobbs.)

advanced to 42°, betrays a very similar rapid retreat (see fig. 29).

Connected with this unique rapidity of dissolution of the Keewatin glacier is perhaps the unique irregularity of the lobe outlines, both at the beginning and near the end of the glacier. The moraines of the James River lobe suggest that great surface streams of thaw water pouring off the front may have produced the crenulations in the lobe outline which are unparalleled elsewhere. However, the nearest approach is to be found in the lobe outlines in northeastern Minnesota in the waning stage of the same glacier (see map 8).

The unparalleled dissolution of the James River and Des Moines lobes is in a large way to be explained by the fact that here only in the entire glaciated area the lobes had pushed out as shrunken arms athwart the tracks of the low pressure areas of the planetary wind system. Elsewhere in their reconquest of the glacier, the winds bearing rain could only *invade* the glacier territory from the west for an attack upon the glacial anticyclone above the ice. Here, however, they could dominate completely and, winter and summer alike, could sweep across the lobes with catastrophic consequences in quick dissolution of the ice of the eastern flank (see p. 374). A further proof of this debacle will be given below in the late history of the "Iowan."

"Iowan Till" an Outwash from the Des Moines Lobe of the Late Wisconsin Glaciation

The glacial anticyclone has thrown much light upon the nature of the "Iowan Drift" formation, about which controversy has raged for many years, but with apparent general agreement now

MAP 8. Moraines of the southern portion of the Keewatin glacier (after reports of Upham and maps of Leverett and Sardeson).

reached that this formation represents an earlier Wisconsin glacier invasion. By some it had

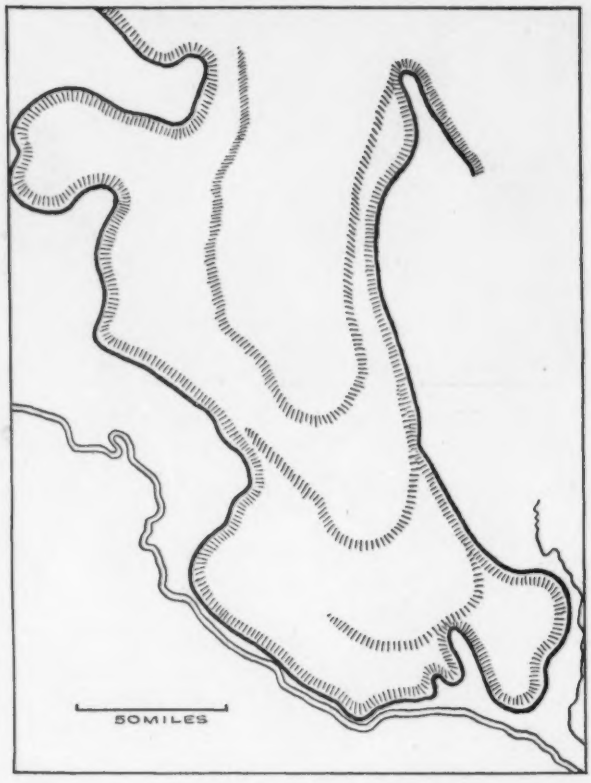


FIG. 29. Moraines of the James River lobe of the late Wisconsin stage of the Keewatin glacier (after Todd with additions and corrections by Leverett).

earlier been thought to be a glaciation nearly as old as the Illinoian.

Now studied with knowledge of the glacial anticyclone, the main area of it at least appears to be no glaciation at all, but an outwash from the Des Moines lobe of the late Wisconsin glaciation.

That the "Iowan" is not a glacier seems to be clear on several grounds. These are:

1. *Outline.*—The outline of the formation bears no resemblance to that of a glacial formation. Its dimensions, which are those of a lobe would require a quite different front.

2. *Materials.*—The deposits are not glacial till-boulder clay.

3. *Upper surface.*—This lacks the characteristic glacial features: ridges, hummocks, and kettles. There are no moraines of any kind. In place of a marginal moraine, the deposits at the border thin out gradually.

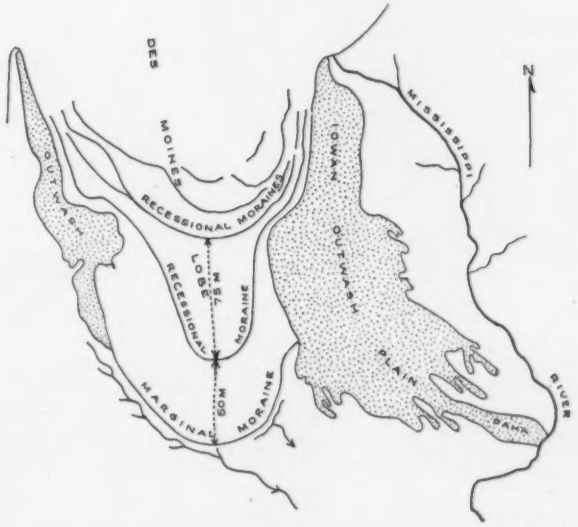
The "Iowan" is an outwash formation connected with the Des Moines lobe of the Keewatin glacier. The grounds for this conclusion are:

1. *Position.*—The formation borders the Des Moines lobe (see map 9).

2. *Outline.*—The outline is that characteristic of flood deposits on flattish, gently inclined slopes, such as foothills to a range—pediments (see fig. 24*D*, p. 389).

3. *Underlying trough.*—The deposits lie in a flat shallow trough on the surface of the Kansan drift, and this trough has an axis directed with the medial line of the area. This direction is southeastward, and the gradient of the axis is about 3 feet to the mile. A short distance beyond the southern rim of this trough the gradient changes to a southerly one. The fact that loess here lies over the Kansan deposits within the interstream areas has protected the upper surface from erosion, and makes it possible for the surface of the shallow trough to be reconstructed. The "Iowan" thus is an illustration of case IV of drainage extramarginal to the lobate area (see fig. 23, p. 388).

4. *Materials.*—The deposits are imperfectly stratified sands and gravels, with included pebble beds and ventifact boulders. The sections chosen as typical by the Iowa Geological Survey are here given in figures 30 and 31. The Iowa State University has a large collection of photographs of other sections, but they show little difference from the two typical ones here represented. The principal pebble band can be followed for long distances as a horizon marker. The surface of the deposit is strewn



MAP 9. The Des Moines lobe and its attached outwash area. Outlines of the lobe after Kay and moraines from Upham's description.

FIG. 30. Section through "Iowan" outwash with cover of 2 feet of loess. The principal pebble band is at the surface of the outwash deposits, but others less marked can be made out below. This locality is about 40 miles distant from the Des Moines lobe and near Denver Junction, Jefferson Township, Bremer County, Iowa. (After Kay.)

FIG. 31. Section through "Iowan" outwash with about 4 feet of the loess veneer above. Pebble bands can be easily followed. The size of the ventifact boulders can be gauged by the hand level. This locality is about 100 miles from the Des Moines lobe margin and in sections 1 and 2, Fremont Township, Cedar County, Iowa. (After Kay.)

with boulders large and small, among which granite predominates.

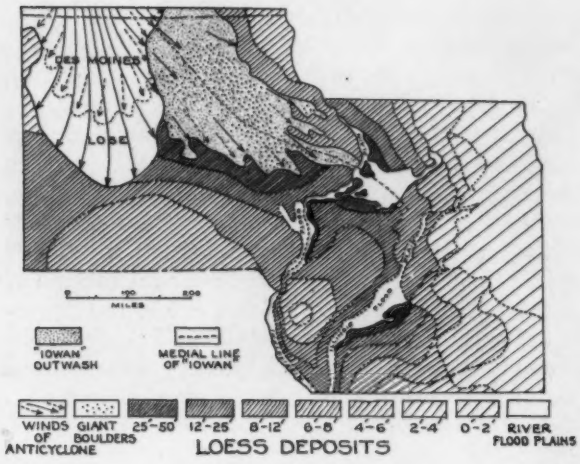
5. *Surrounding rim of loess.*—Surrounding the formation and forming an outer rim to it is a

FIG. 32. View looking down on the flat surface of the "Iowan" outwash plain from the raised rim of loess at a point north of North Liberty, Johnson County, Iowa. (Photo by W. H. Hobbs.)

thick deposit of loess which rises on a steep slope and makes of the "Iowan" surface a panlike flat-bottomed basin with a sharply raised rim. This surrounding deposit of loess has a maximum thickness at the eastern edge of the "Iowan" of 53 feet, and more than 25 feet on the southern margin throughout (see especially map 10, p. 397). This rim of the "Iowan" is that described by Chamberlin and Calvin on preceding pages. (See fig. 32.) Its position marks the nearest approach of vegetation to the "Iowan" while the outwash was swept by floodings. Its thickness falls off from the margin, but it has a wide distribution unsymmetrical to the medial line of the "Iowan" and its extension southeastward into Illinois, as shown in map 10.[65] The map shows also the late Wisconsin and post-Wisconsin redistribution of the loess from river deposits, especially noteworthy east of the broad flood plain of the Illinois River. The main distribution seems to be explained by the large area of the "Iowan" outwash—with but two parallels anywhere within the entire glaciated area (see pp. 399, 401)—and also by the fact that the winter northwest storms of the planetary system, when they had prevailed over the glacial anticyclone on the west flank of the Des Moines lobe, overrode the cold winds of the east flank and so caused a deluge of rain.

6. *Later veneer of loess.*—The main loess deposits and the "Iowan" outwash are alike veneered by a light deposit of loess which thins

[65] Smith, Guy D. Illinois loess, variations in its properties and distribution. *Agric. Exper. Sta. Univ. Illinois, Bull.* 490, fig. 3, 1942.



MAP 10. Loess distribution about the "Iowan" outwash. (After Leverett in Iowa and after Guy D. Smith in Illinois.)

out as the lobe is approached (compare figs. 18 and 29 and map 9) and dies out in Worth and Cerro Gordo Counties before the lobe is reached. This deposit is believed to have been laid down as the glacier front retired northward and the flooded area was reduced in area so that vegetation could gradually encroach upon the plain from its outer limits.

7. *Boulder-strewn surface.*—On the flat surface of the "Iowan" plain are strewn boulders in such numbers as to make some parts unsuited for profitable farming. In other portions the farmers have hauled the boulders into piles. In several areas which I have seen, the evidence of sand blasting upon these boulders is very marked (see fig. 7, p. 372). These boulders have probably been carried by ice blocks from the Des Moines glacier[66] (fig. 33).

8. *Giant boulders on the "Iowan."*—Many of the boulders on the "Iowan" plain are so large as to be perhaps the largest anywhere transported in connection with glaciation (see figs. 34 and 35). One in Rivington Township, Floyd County, some 25 miles outside the margin of the Des Moines lobe, is 50 feet long and 40 feet wide and rises 11½ feet above the ground. It must weigh well over 1,000 tons.[67] They generally lie in swales, probably explained by the ice slabs which floated them keeping off the outwash and later melting to form the depression. To explain the transportation of boulders of this size, most extraordinary conditions are called for. Their migration clearly came at the close of the Wisconsin when, as described in the last paragraph, there occurred the debacle of dissolution of the dead ice stranded between the mineral ridge and the next succeeding recessional moraine of the Des Moines lobe. Already much thinned, the dead ice sheet was probably divided by thaw-water channels into ice slabs, some of which doubtless had dimensions measured in many hundreds of feet. The "Iowan" plain was a flat-bottomed basin everywhere rimmed by a steep wall of loess and contracted to a bottleneck at its outlet into the swollen Mississippi at the far southeastern end.

In this latest stage of the dissolution of the lobe the vigor of the glacial anticyclone had been

FIG. 33. Boulders on the flat surface of the "Iowan" plain. This locality is distant from the margin of the Des Moines lobe about 75 miles, in Winthrop, Buchanan County, Iowa. (Photo by Samuel Calvin.)

FIG. 34. Giant granite boulder stranded on the "Iowan" plain. This locality is distant about 8 miles from the Des Moines border and is in Pleasant Valley Township, Grundy County, Iowa. (Photo by James H. Lees.)

[66] Individual boulders weighing 300 tons were transported from Ford Canyon in Utah onto the foothill slope in the great flood of 1930 (Floods and acceleration erosion in northern Utah, *U. S. Dept. Agric., Misc. Publ.* 196: 5). The largest on the "Iowan" is thrice that size but was floated by ice slabs in floods and propelled by the wind.

[67] Alden, W. C., and M. M. Leighton. The Iowan drift. *Geol. Survey Iowa Ann. Rept.* 26, ch. V, 1915.

so reduced that the winds of the planetary system advanced over the western flank in opposition to the easterly anticyclonic winds there, and, topping the divide, overrode the cold westerly anticyclonic winds of the east flank. This must have resulted in extremely heavy rains[68] which would have been restricted, however, to the easterly flank, and the water would pour down over the ice surface on the easterly slopes.

The slower wasting of the lobe which precedes the debacle when the planetary winds have overridden the anticyclone, takes place entirely on the western flank where the planetary winds invade the area above the lobe for greater and greater distances. Under this action the ice divide migrates to the eastward and the western slope takes on a flatter and flatter gradient. When, however, the area invaded extends beyond the divide, the planetary winds highly charged with moisture, now no longer opposed, largely override the westerly winds of the eastern flank with heavy precipitation. Slow wasting of the western flank is now succeeded by rapid dissolution of the eastern slope and the divide now migrates westward.

As we are to see, the distribution of the areas of heavy outwash deposits shows that while these cover very small areas off the western slopes of ice lobes, they are by contrast broadly extended off the easterly slopes (see pp. 399 and 402). There is in this conclusive proof that the earlier liquidation on the western slopes did not reach down into the bottom layers with englacial debris.

9. *Forest beds in the "Iowan" outwash.*—When the rapid lowering of the upper surface of the eastern slope of the Des Moines lobe had descended into the bottom layers with their englacial rock debris, a veneer of bouldery clay formed on the surface, and where forest vegetation had already developed outside the ice margin, the conditions were favorable for encroachment of the forests for a greater or less distance over the glacier, much as has happened in our day over the front of the Malaspina glacier in Alaska. Still later the forest cover on the Des Moines lobe would be undermined as water channels dissected the surface. The trees would then be progressively uprooted and carried out as flotsam in the floods to become stranded in the shallower water near the margin of the flooded area.

On the northeastern margin of the "Iowan" in Fayette County, the outwash deposits are underlaid by a "forest bed" layer several feet in thickness. This layer is made up of logs, stumps, branches, and roots of trees together with an inky black decomposition residue.[69] While the forest bed is formed near the margin of the deposit, the giant boulders are found aggregated within a central area (see fig. 33), probably because the ice slabs in which they were floated required a depth of water. A giant boulder on the till of the Des Moines lobe itself is shown in figure 35.

FIG. 35. Giant boulder of granite on the till of the Des Moines lobe 50 miles inside the border on Prairie Creek, Webster County, Iowa. (Photo by Samuel Calvin.)

10. *Boulders of "Iowan" are of types similar to those of the Des Moines lobe.*—The boulders of the "Iowan" surface represent a variety of materials, in which, however, granite greatly predominates; and these varieties do not differ materially from those in the till of the Des Moines lobe.

11. *The paha at the bottleneck.*—Long straight ridges of sand with a veneer of loess were first described by McGee at the extreme southeastern limit of the "Iowan," and they have been the subject of many later descriptions. Their origin now appears to have been connected with the bottleneck outlet of the floods from the "Iowan" into the much swollen Mississippi of that period. The current was checked before it entered the river and laid down heavy deposits of sand within the outlet, and pushing out, crowded the river to

[68] A mild indication of what results when warm saturated air currents override cold air masses is furnished by winds off the Pacific that pass eastward over cold air masses on the North American continent.

[69] McGee, W J. The Pleistocene history of northeastern Iowa. *U. S. Geol. Survey, 11th Ann. Rept.*, pt. 1: 486, 541, 1891.

the eastward so as to produce the great bend north of Clinton. The sand grains became smaller as the glacier front retired northward and the floods subsided. Later, when the Mississippi floods subsided, the channels in the outlet cut gorges in their own sand deposits and left straight drumlinoid sand ridges between them which are the paha. Still later, when vegetation had taken root, in common with the "Iowan" and the surrounding heavy loess deposits, they received a veneer of loess.

Dissolution of the Scioto Lobe

The Labradorean glacier underwent a slow dissolution from the west as the planetary wind system invaded the waning anticyclone for greater and greater distances. This is clearly revealed by the spacing of the recessional moraines, while a stable ice border prevailed on the east, and only less so on the south, where the general trend of the ice border was nearly parallel to the storm tracks (map 7, p. 393).[70] When, however, in the eastward recession of the Labradorean glacier's west front, the eastward-sloping flank of the Scioto lobe had been reached, this lobe came under conditions similar to those in the late history of the Des Moines lobe of the Keewatin glacier just described.

As the planetary storms gained the medial divide and so obtained a local mastery of the anticyclone, they accomplished an overriding of it and consequent downpours of rain on the eastern and southern slopes. This transferred the dissolution from the western slopes, and greatly accelerated the tempo of the ice wastage. As the level of the ice surface now descended into the bottom debris layers, the outwash deposits began to be laid down; though here not upon a featureless plain but in the valleys of a dissected upland. As a consequence, the valleys of all rivers flowing from the ice border were filled with outwash to depths up to a maximum of 300 feet, with channels choked and reversal of drainage on a scale nowhere else parallelled within the glaciated area (see map 11). Boulders were carried out on the outwash by ice blocks, as elsewhere so widely observed on outwash plains.

That there was a vast expanse of dead ice at the front of the lobe is shown by the absence of recessional moraines between Circleville at the inner margin of the terminal moraine series and the Tekonsha moraine 20 miles north of Columbus (an interval of about 60 miles), after which a new moraine series begins where protection from planetary winds was afforded by ice masses lying to the eastward. (See map 1, p. 374, for comparison with Miami and White River lobes.) The parallel with the Des Moines lobe of the Keewatin glacier is here very close (compare maps 9 and 11).

To the south and east of the lobe between the outwash-filled valleys, patches of loess are still retained on hilltops between the valleys. Loess, however, seems not to have been found east of Parkersburg, West Virginia.

Though the outwash deposits choke all river valleys to the east and south of the Scioto lobe, they are perhaps best observed in the broad Licking River Valley near Hanover, 9 miles east of Newark, Ohio (*A* of map 11). Apparently similar conditions had obtained when the Illinoian glacier was in this vicinity. The outwash of the Wisconsin glacier fills the valley of the Licking near Hanover to a depth of 300 feet, with surface 800 feet above tide. The Illinoian glacier had its borders on higher ground to the eastward, and so its outwash reaches to the 900-foot contour just east of the Wisconsin outwash.[71]

Rapid Liquidation of the Dying Labradorean Glacier in Southern New England

East of Ohio the Wisconsin front passes into the Appalachian highland, already in plain view from the Scioto lobe, and here it loses its lobate outline and takes on the character of the front of contained existing continental glaciers. Unable to spread out freely, as it did in the Mississippi Valley, it here doubtless rose on steeper slopes to much higher levels. Its border profile may have more resembled sections *A′* and *B′* than *A*–*C* in figure 21. Its nearly rectilinear outline was directed east-southeasterly for 250 miles, or as far as the mouth of the Hudson, but there it made a sharp turn and was directed east-northeast to and beyond Nantucket. This

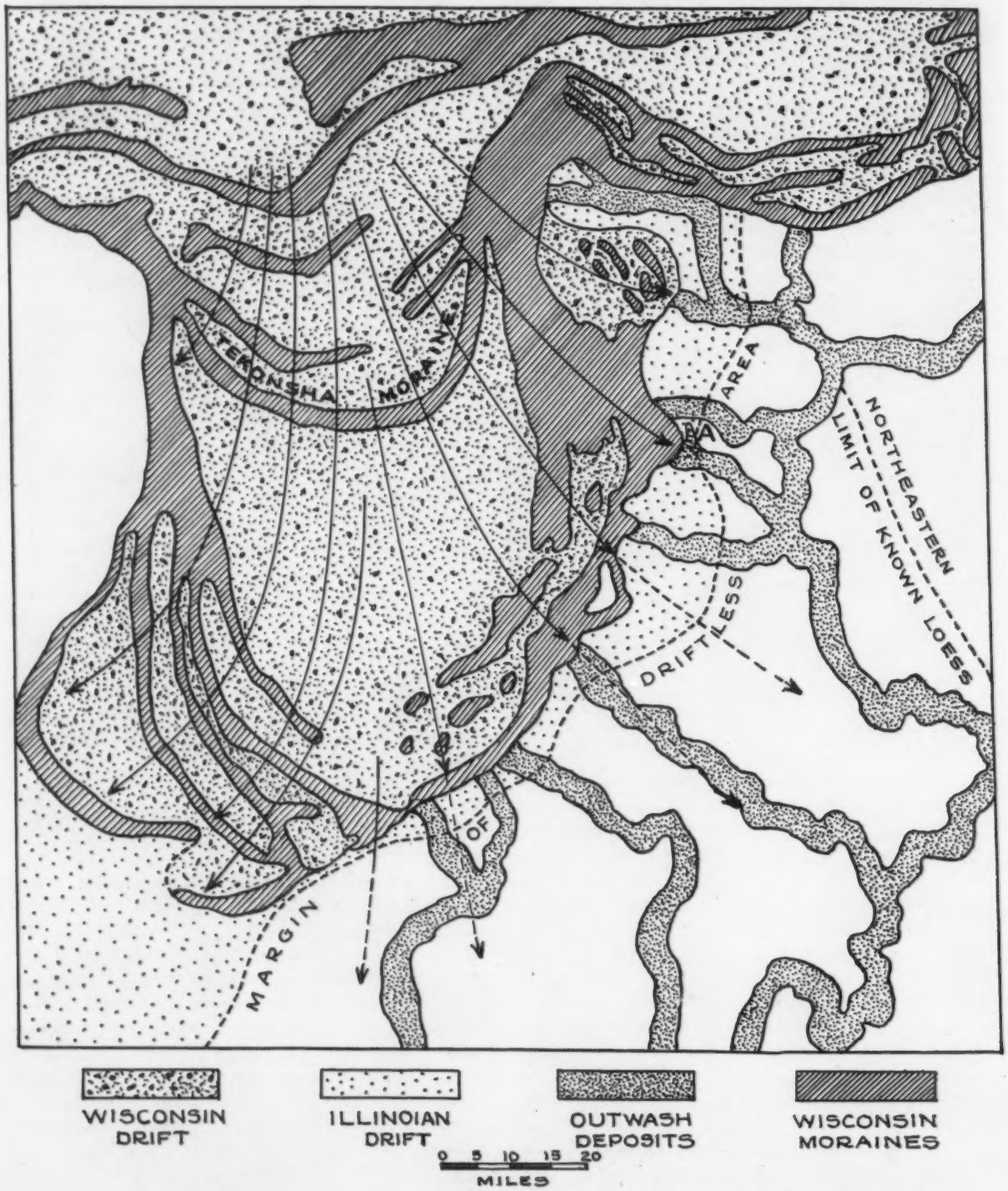
[70] Leverett, Frank. Glacial formations and drainage eatures of the Erie and Ohio basins. *U. S. Geol. Survey Mon.* **41**: pls. II and XIII, 1902.

—— Illinoian drift in eastern Ohio. *Am. Jour. Sci.* **237** (11): 834–839, fig. A, 1939.

—— Gravel outwash near Chillicothe, Ohio. *Science* **95** (2473): 528–529, 1942.

[71] Leverett, Frank. Illinoian drift in eastern Ohio. *Am. Jour. Sci.* **237** (11): 834–839, fig. A, 1939.

—— Gravel outwash near Chillicothe, Ohio. *Science* **95** (2473): 528–529, 1942.



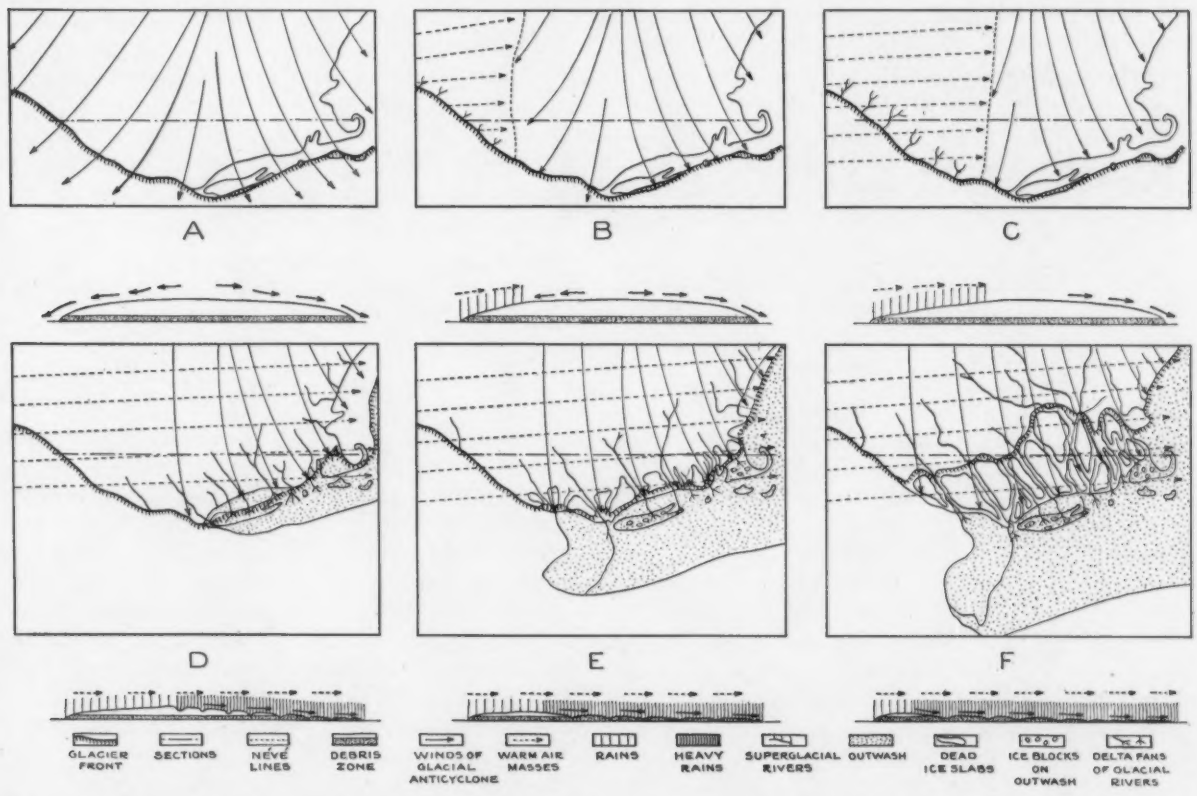
MAP 11. The Scioto lobe of the Labradorean glacier. Based on maps by Leverett published in 1902, but with corrections by him for this paper.

entire front from Ohio to Nantucket seems to have been the most stable of any part of the Labradorean glacier. This is only partly because its steep front took its course so nearly parallel to the tracks of the planetary storms and so might perhaps have effected a diversion of them. Until the Scioto glacier lobe had been disposed of in the ultimate liquidation of the lobate western portion of the Labradorean glacier, the storms which reached the eastern non-lobate section had been already robbed of their moisture (see map 1).

With the disappearance of the last bastion of defense in the melting of the Scioto lobe during the very late Wisconsin period, the New York - Pennsylvania front, which had held from the beginning of that period, began to be invaded, and its liquidation was begun. The divide of the ice surface then extended northward from the salient at the mouth of the Hudson in the direction of the high center of alimentation in Labrador, a distance a third less than that to the center from the earlier front in Illinois and Wisconsin.

When the eastward invasion by the air masses of the planetary system had reached this divide, they would have swept as a vast canopy over the anticyclonic winds of the entire glacier surface in southern New England and still farther to the eastward over any occupying the western border of the Gulf of Maine. The downpours of rain from this canopy evidently produced liquidation of the glacier on a scale unprecedented elsewhere. The outwash after the bottom layers had been reached spread southward from the salient at the site of New York City across the entire state of New Jersey and the estuary of the Delaware. To the east they not only covered most of Long Island, Martha's Vineyard, Block Island, Nantucket, Cape Cod, and the area about Buzzard's Bay, but they extended southward for 150 miles over the continental shelf, which was at the time a part of the continent (see map 12).[72] This material has not been differentiated for the

[72] Shepard, F. P., and G. V. Cohee. Continental shelf sediments off the Mid-Atlantic States. *Bull. Geol. Soc. America* **47**: 441–458, 4 pl., 2 fig., 1936.



MAP 12. Successive maps to illustrate the final dissolution of the non-lobate portion of the Labradorean glacier. The superglacial streams have determined the pattern of the last Wisconsin drainage. Maps *E* and *F* are in part schematic.

glacial periods, as has that on Long Island,[73] but some probably belongs to the Jerseyan.

The even front of the glacier in southern New England favored the formation of a series of superglacial rivers, which, descending the southern slope in a southeasterly direction, broke through the marginal moraines and spread glacio-alluvial fans which, because of the violence of the floods, moved out some distance before coalescing to form a gigantic glacial pediment.[74] This southward sloping plain occupies the southern three-quarters of Long Island, and its extension in southeastern New England (Mashpee Plain) has much the same character.[75] On Long Island, particularly, the outwash is so abundant that the outer moraine is largely of gravel and a new term, "stratified moraine," was necessary to describe it. The inner moraine is nearly overtopped by outwash and, instead of constituting a continuous ridge of till, is interrupted by the glacial rivers so as to be in part a broken line of till islands. No outwash of this character on such a scale has been observed elsewhere (see map 12).

Such rapid liquidation of glacial ice is probably explained by the relatively weak anticyclone in this final stage, which at the end of minor climatic cycles was not powerful enough to build up new active fronts behind the dead ice at the actual front. For this reason no very definite recessional moraines were laid down. That the winds over the outwash were still vigorous when the active front was on Long Island is attested by the ventifacts, perhaps the greatest garden of such boulders and pebbles anywhere in the glaciated area.

The final dissolution of the ice front yielded great ice blocks and slabs, and the glacial pediment is everywhere spotted by pits, large and small, both on Long Island and in the Buzzard's Bay area. The pits indicate the loci of stranded or buried ice blocks which were later melted.

Reference has already been made to the extension of the Pleistocene silt far out on the continental shelf and to the silts of late Wisconsin age (loess) observed in borings still farther out (see *antea*, p. 380).[76]

In this general treatment no attempt has been made to carry the study of the glacial anticyclone to any but the latest of the glacial invasions of North America.

In conclusion I wish to acknowledge my very great indebtedness to Dr. Frank Leverett, whose vast knowledge of glaciation has been always at my disposal, and also to Dr. George F. Kay for much help on the Iowan area. Without taking any responsibility for views here expressed, both these gentlemen have given assistance in the most cordial spirit of co-operation.

[73] Flint, R. F. How many glacial stages are recorded in New England. *Jour. Geol.* **43**: 771–777, 1935.

[74] Fuller, M. L. The geology of Long Island, New York. *U. S. Geol. Survey Prof. Paper* 82: xiv and 231, especially the large glacial map of pl. I (in pocket), 1914.

[75] Mather, K. F., R. P. Goldthwait, and L. R. Thiesmeyer. Pleistocene geology of western Cape Cod, Massachusetts. *Bull. Geol. Soc. America* **53**: 1151–1159, 1942.

[76] See also H. T. U. Smith and H. J. Fraser. Loess in the vicinity of Boston, Massachusetts. *Am. Jour. Sci.* **30**: 16–32, 1935.

NOTES ON THE MAMMAL-BEARING TERTIARY OF SOUTH AMERICA

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THE following brief notes are supplementary to a recent review of the mammal-bearing Tertiary of South America (Simpson, 1940). They bring together some new data and references to two brief publications accidentally omitted, thus completing the review and bringing it essentially up to date.

ARGENTINA

The almost completely barren Llanos formation ("formación de los Llanos") of the Province of San Luis (western pampas region, directly east of Mendoza) can now be approximately correlated and inserted in the Argentine sequence of mammal-bearing formations. Although only three fully identifiable mammals have been found, description of the most recently discovered of these by Bordas (1941) suggests that their age is about Chasicoan. Their level is thus approximately synchronous with Chiquimil B of the classic Catamarca series and probably older than any definitely correlated mammal-bearing horizon in the near-by Huayquerías, Province of Mendoza.

The problem of the Collón-curá tuffs and of a mooted Colloncuran stage is somewhat advanced, without being solved, by a recent report by Feruglio (1941). He designates and discusses various exposures of these beds in the subandine zone of the San Carlos de Bariloche Quadrangle, including Lake Nahuel-Huapí and the region east and south of it. These tuffs occur in isolated and generally thin patches in depressions on older beds, an Eogene andesitic series and the Patagonian marine beds. The type of occurrence makes stratigraphic leveling or determination of succession impossible. The contemporaneity of the various exposures, possible span covered, and place in the established sequence can be determined only by fossils, and the discoveries of these are as yet entirely insufficient for positive conclusions. Scanty mammals from some localities have been identified as definitely Santacrucian (*e.g.*, Ñorquin-có), from others as definitely Friasian (*e.g.*, Comallo). The argument for a Colloncuran stage between Santacrucian and Friasian would thus seem to be that beds supposedly of the same age but identified in two different places as of two different ages are to be considered intermediate between the latter ages. The logic of such a conclusion is plainly faulty. On present evidence, the reasonable alternatives are:

1. One of the two conflicting age determinations is incorrect. If so, the Santacrucian identifications are more likely to be wrong. In that case, the Collón-curá tuffs would appear to be of Friasian age as far as now known.

2. Both identifications are correct. In that case the Collón-curá tuffs are a complex of different ages, Santacrucian to Friasian, at least. It would then be probable that some of them are intermediate between these two ages, but if so, the characters of the hypothetical intermediate fauna and the possibility and advisability of recognizing an intermediate age have yet to be determined. The advisability of calling that age "Colloncuran" is also questionable if the formation now called Collón-curá is not wholly or mainly of that age.

In either case, it is hard to see how the supposed Colloncuran stage can now be defined. It has no practical present meaning and may best be dropped from the sequence until or unless objectively established under this or another name.

CHILE

Reference to Tertiary mammals in Chile was omitted in the previous review. To the best of my present knowledge, two such discoveries have been made, one briefly and somewhat obscurely mentioned by Hemmer (1935) and one recently described by me (Simpson, 1941). Hemmer's specimen, identified by C. L. Gazin as *Astrapotherium magnum*, was found near the Laguna del Toro, latitude about 52° 46′ S. The second specimen, named *Nematherium birdi* by me, was found by Junius Bird near Laguna Blanca, latitude 52° 26′ S. The localities are about 38 kilometers apart, and both are near the boundary of Argentine Patagonia (Territory of Santa

Cruz). The beds have been called the Palomares formation (or strata) by Hemmer. These mammals indicate Santacrucian age and suggest that the Palomares is simply part of the Santa Cruz formation that here happens to extend for a few miles beyond the political boundary.

Brazil

In the previous review the occurrence of a late Miocene rodent, *Phoberomys*, in Brazil was mentioned on the basis of unpublished observations by Patterson (Simpson, 1940: 703). The data have now been published (Patterson, 1942), and the specimen has been named *Phoberomys bordasi* Patterson. Patterson locates the fossil near the base of the "Brown beds" series of Singewald (1937) and correlates the horizon as approximately Mesopotamian, probably latest Miocene, in age. The "Brown beds" as a whole may thus be more or less equivalent to the Araucanian group of Catamarca, Argentina, which also has a Mesopotamian equivalent near the base.

Peru

In the same publication Patterson (1942) has also provided the promised redescription of *Griphodon*, identified as a pyrothere suggesting age intermediate between Mustersan and Deseadan. The locality has been in some doubt and is given by Patterson, from various other sources, as near a place variously called Chepeza, Chipeda, and Chipaza, below Yurimaguas on the Huallaga River (more precisely, a few hundred feet up a small tributary entering the Huallaga a short distance below a farm house called Chiococa), in far southwestern Loreto, Peru. The fossil was in the thick series called the "Red beds" by Singewald (1937), which thus contain a late Eocene or early Oligocene level, but these beds are very thick, up to 8,000 feet, and evidently cover a long span of time. The position of *Griphodon* within the series is unknown.

Colombia

In the previous review (Simpson, 1940: 704), I noted the occurrence in Colombia of astrapotheres allied to *Xenastrapotherium*, but I overlooked the fact that some material of these had been described by Cabrera (1929) and given the name *Xenastrapotherium kraglievichi*.

References

Bordas, A. 1941. Nuevos restos fósiles de la formación de los Llanos (San Luis). *Physis* **19**: 23–27.

Cabrera, A. 1929. Un astrapotérido de Colombia. *Physis* **9**: 436–439.

Feruglio, E. 1941. Nota preliminar sobre la hoja geológica "San Carlos de Bariloche" (Patagonia). *Bol. Inf. Petrol.* [Buenos Aires] 200: 27–64.

Hemmer, A. 1935. Sobre la presencia de *Astrapotherium magnum* Ameghino en los estratos de Palomares en la región de Magallanes. *Bol. Minas Petrol.* [Santiago de Chile] **5** (52): 534.

Patterson, B. 1942. Two Tertiary mammals from northern South America. *Am. Mus. Novitates* 1173: 1–7.

Simpson, G. G. 1940. Review of the mammal-bearing Tertiary of South America. *Proc. Am. Philos. Soc.* **83**: 649–709.

—— 1941. A Miocene sloth from southern Chile. *Am. Mus. Novitates* 1156: 1–6.

Singewald, J. T., Jr. 1937. Geological exploration between upper Juruá River, Brazil, and middle Ucayali River, Peru. *Bull. Am. Assoc. Petrol. Geol.* **21**: 1347–1350.

GENETIC AND SEASONAL VARIATIONS OF ORANGE WING-COLOR IN *COLIAS* BUTTERFLIES

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ABSTRACT

Experiments and observations are recorded on controlled and natural hybridization between the wide-spread orange butterfly, *Colias eurytheme*, of the Western States and two minor yellow species distinct from it but merging into each other on the Great Plains east of the Rocky Mountains. These are *C. eriphyle*, a far-western mountain species, and *C. philodice*, of the Mississippi Valley and Eastern States. Wherever *eurytheme* is abundant in the presence of either yellow species, hybridization sometimes occurs, easily detected in midsummer, especially in the male, by the paler orange wing-color of the hybrid. Immigration of *eurytheme* into a population of pure *philodice* (as in New Hampshire) has resulted in equal numbers of pure immigrants and hybrids (fig. 4: 1.5 percent of a 648 population).

Eurytheme females (Ariz.) mated readily with *philodice* (N. H.) males. The F_1 broods (fig. 1) were of fair or large size, but 8 of 9 F_1 matings in 1913 were sterile, and the ninth gave only 19 F_2 offspring (pl. A). Backcross matings, F_1♂ × *eurytheme* ♀, however, in 4 out of 7 matings were fertile with numerous offspring. Matings in the reverse order (*philodice* ♀ × *eurytheme* ♂) were in 1914 again difficult to obtain, but 2 of such cross-matings were made, as compared with 25 brother-sister *eurytheme* matings. These were 1914 a and c (fig. 1). Though F_1 hybrids from either reciprocal cross mated together readily, there was much sterility. The 3 F_2 broods in 1914 were all small; a backcross to *philodice* (pl. B) was larger (60). Sterility was not restricted to either sex. Red (orange) is incompletely dominant (intermediate), roughly "apricot yellow" (Ridgway) in summer (pl. A). The range in orange variations in F_1 hybrids was much less than in pure *eurytheme*. F_1 broods were measured and compared as to seasonal differences in intensity of orange (fig. 2). F_2 broods showed segregation into orange and yellow roughly on a 3:1 basis (pl. A). Late fall seasonal conditions reduced orange intensity equally throughout the wide F_2 and backcross ranges without disturbing segregation. Coefficients of variability in red in *eurytheme*, F_1, F_2, and both types of backcross are compared. The pronounced seasonal reduction in redness and size under late-fall conditions was studied in relation to temperature and light (shortness of day). This reduction in redness and size was due not so much to low temperatures and diminished illumination as to condition of the white clover food-plant. All these factors control activity in feeding, nutrition, and rate of metabolism of the caterpillar, and thus diminish wing size and intensity of orange pigmentation of the butterfly while, simultaneously, the melanic under-surface pigmentation is intensified (darkened).

The historical basis of frequent confusion of *C. eriphyle* with seasonal phases of *eurytheme* is discussed. Measurements of traces of red in *eriphyle* females show gradual increase in intensity from the Kansas and Nebraska *philodice* (*eriphyle*) stocks to and through the mountain races of true *eriphyle* from Colorado, Wyoming, and Alberta (fig. 6). Differences between white females of Kansas *eurytheme* and *philodice* (fig. 7) are described. Mating experiments with Kansas stocks show incompatibility between *philodice* and *eurytheme* but not any between Kansas and New Hampshire *philodice*. A natural hybrid brood from a wild Kansas *eurytheme* female was measured (fig. 8) for its extreme variations in redness, which, in range and coefficient of variation, resembled a backcross somewhat like that shown in plate B.

The Colorado stock (fig. 7) was started from a brood of *eriphyle* (nearly 80 percent female) raised indoors on white clover and a brood of the (larger) *eurytheme* raised outdoors on alfalfa. Seven *eriphyle* females mated with New Hampshire *philodice* males; the one mating tested was fertile; 6 *eriphyle inter se* matings and 3 cross-matings with

eurytheme males occurred. One of these cross-matings was fertile. There was no observed tendency in any of the Colorado caterpillars to fast. The sex apathy of the 14 females of Colorado *eurytheme* was unusual and unexplained. Size differences in wing expanse between the *eriphyle* and *eurytheme* were measured. Offspring of 2 Wyoming *eriphyle* females, as young caterpillars, fasted and became dormant in September. Those of a third did not; from them came two generations, one maturing in October and May, followed by the next in June-July; the two showed marked seasonal differences in size and color. The early-summer females, though active and healthy, were evidently sexually immature (emerged earlier perhaps than they would have in Wyoming) and no matings of any kind were secured. Two autumn broods of *eriphyle* from Alberta were raised; no mating experiments were recorded. Natural *eurytheme* × *eriphyle* hybrids appear to be rather common in north central Oregon and eastern California; the same is said to be true recently of *eurytheme* × *philodice* hybrids in the Middle Atlantic States.

Introduction

Regarding the kaleidoscopic array of species and subspecies of the genus *Colias* in the Western United States and Canada, Holland (1910) states: "It requires almost as much skill to distinguish them as is required to discriminate between the different species of willows, asters and goldenrods." In *Colias*, as in these notoriously variable plants, mutation and hybridization are active in producing minor species and geographical races.

By far the most wide-ranging and one of the most variable species of *Colias* in America is *C. eurytheme* Boisduval, popularly known as the orange-sulphur, or alfalfa, butterfly. In the United States its range now extends from the Pacific in diminishing frequency to the Atlantic Ocean. Northward, its habitat follows the Rocky Mountains into an undefined region in western British America and reaches Hudson Bay; southward, it extends into Mexico. Eastward from the Pacific, *eurytheme* ranges over the Mississippi Valley wherever alfalfa and various clovers grow; recently it has passed the Alleghenies to the Middle Atlantic States and is now very slowly extending its range into northern New England.

Locally associated with *C. eurytheme* and very probably derived from it are two minor, yellow species, *C. philodice* and *C. eriphyle*.

C. philodice Godart, the very common "clouded sulphur" or clover butterfly, ranges westward from the Atlantic roughly as far as the Rocky Mountains. On the plains of Kansas and Nebraska, just east of the Rockies, it shows one of the characteristics, at least, of the western yellow *C. eriphyle* (orange flush under the forewings of the female).

The name *eriphyle* was first applied by W. H. Edwards (1897) to canary-yellow specimens from Lake La Hache in south central British Columbia. The species is distributed widely over the mountain states from Montana, Wyoming, and Colorado to the Sierra Nevada Range, beyond which westward to the coast it has rarely been found.

I have raised large broods of *eriphyle* (fig. 7) at Hanover, N. H., from fertile females sent from Alberta (Midnapore, near Calgary), Colorado (Tolland), and Wyoming (Centennial). Those of the same seasonal generation as *eurytheme* are smaller than in the latter species. The male has nearly the same pale yellow tint above as in *philodice*, and, as is not unusual among *Colias* species, looks superficially like that male. The black border in some *eriphyle* stocks is relatively wider than in *philodice*, but this trait though hereditary is controlled somewhat by seasonal conditions (narrower in spring and fall).

The color pattern and ground color of the female are more distinctive. The dark border of the hind wings in the female *eriphyle*, as in *philodice*, is narrower and less broken by spots than in *eurytheme*. The faint orange flush upon the upper surface of the wings of some of the summer generation females of *eriphyle* (fig. 6) and on the lower surface of the forewings in that sex generally, suggests a close affinity of this western mountain yellow species with *eurytheme;* pure *philodice* females lack such traces of orange on their upper wing surface.

Broods of western yellows (*philodice*), the mothers of which came from the plains of Kansas and Nebraska, constantly retain traces of orange *under* the forewings of the female (fig. 6). In spite of this point of resemblance to *eriphyle* of the neighboring Rocky Mountain States, I have come to regard them as *philodice*, which farther eastward has lost even this vestige of orange.

Both yellow species, however, were probably derived from the more vigorous, highly colored *Colias eurytheme*.

With this brief description and summary of observations on *eriphyle*, which will be elaborated in a later section of this paper, we shall direct our attention first to *C. philodice* of New Hampshire and its hybridization with *eurytheme*. Unless otherwise stated, the *philodice* of these experiments refers to the sulphur-yellow stock of this region.

Some of the results recorded in this paper were published in preliminary form (Gerould, 1913: 113–114, and 1914: 328–330), but more complete treatment required numerical measurements of the intensity of red and yellow pigmentation in the specimens. Such measurements have recently been made by Dr. Hannah T. Croasdale, technical assistant in zoölogy at Dartmouth College, whose intelligent coöperation has made the present publication possible. The instrument used by her was a Levibond "Tintometer," described by the late H. Onslow (1919) and used by him in preparation of a series of papers on inheritance of wing color in moths. The yellow components in these measurements, indicating brightness, are numerically much higher than the red and rather closely correlated with them. Though regularly recorded, they are not included in the present study.

The various stocks of western *Colias* were obtained from wild, fertile females sent by mail in tin cans perforated, and lined with wet blotting-paper sewed securely to the sides. These containers were packed in excelsior to avoid jarring. To prevent mutual interference and overstimulation, not more than two or three butterflies should travel in the same compartment. With plenty of pure moisture and preferably no food, young and vigorous females readily survive a 4- or 5-day journey, but should be fed sweetened water before leaving and immediately upon arriving.

Wild females of *Colias* are usually already fecundated and ready to lay. Caged over 8-inch seed-pans of potted white clover, *Trifolium repens*, with a fresh, constantly moist bouquet of flowers (*e. g.*, phlox when available, never clover) as food, they lay usually abundantly on the white-clover turf in a succession of pots. Caterpillars must be transferred frequently to fresh clover kept healthy and free from aphids. They are very susceptible to the deadly polyhedral disease (wilt, flacherie) and other "silkworm" disorders (*e. g.*, pébrine); by promptly discarding pale, sickly individuals and soaking cages and pots in formalin, the broods were kept fairly healthy. The larvae climb upon the walls of the cage to pupate. Directly upon eclosion, a letter indicating the brood and a superscript number designating the butterfly's position in the list of eclosions of that brood (recorded with date and sex) were written with a stub pen, in India ink mixed with 50 percent alcohol, on the under surface of the right hind wing.

Males and females were then kept in a cool, not too dry or sunny, room in 18-inch-square cages and fed. For mating, a definite number of each sex were put together in a cage exposed to direct sunlight and watched for pairs, which soon after coupling were removed and isolated until copulation was over, usually an hour or more. The female was then placed over her first pot of clover with a bunch of moistened flowers. Low cages (10 inches high × 15 inches × 15 inches, over seed-pans) are best, confining the female near the clover. See also Gerould (1911) and an article in Needham and others (1913).

For western stock I am deeply indebted to Mr. V. L. Wildermuth, of Tempe, Arizona; to the late Prof. Francis Ramaley, of Boulder, Colorado; to the late H. Wolley Dod, of Midnapore, Alberta; to Drs. P. W. and Anna R. Whiting, who sent me in 1922 living stock and many specimens from Nebraska and Wyoming; and to Prof. Roger C. Smith, of Manhattan, Kansas, who repeatedly from 1922 to 1925 supplied me with live butterflies and useful information.

Hybridization Experiments between *eurytheme* and *philodice*

The experiments here described were begun in the autumn of 1912 and continued during the seasons of 1913 and 1914 (June–December). Species-hybrid F_1 caterpillars and pupae of 1912, kept in hibernation in large numbers, did not survive, so that a fresh start was made in June, 1913, and again in 1914 with new stocks of *C. eurytheme* sent from Tempe, near Phoenix, Arizona, by V. L. Wildermuth and R. N. Wilson, of the U. S. Bureau of Entomology.

C. eurytheme is remarkable for its seasonal polymorphism. The members of successive broods differ in size and intensity of orange color; the large, deep-orange summer form, "*amphidusa*," differs strikingly from the small, pale orange-yellow "*ariadne*" of the spring or, in Texas, Louisiana, and southern California, the winter generation. Intermediate between these two phenotypes in size and color is "*keewaydin*." It occurs in California, according to Wright (1906), at all seasons but "probably is more abundant in spring and autumn."

The white (Mendelian dominant) variety of the dimorphic female, in which the ground wing-color is due to a white pigment instead of (recessive) orange-yellow, occurs in the population of *C. eurytheme* in frequency similar to that of

the corresponding female variety in *C. philodice* (Gerould, 1923). Two of the three *eurytheme* females which survived the 4-day journey between Tempe and Hanover in 1913 and one of the two received alive in 1914 were white. It was possible, by crossing their offspring with *philodice*, to study simultaneously inheritance of white and of orange in contrast to yellow.

In the present analysis of the inheritance of the two colors, red and yellow, recessive to white, we shall disregard dominant ♀-whiteness, in the study of which a large part of the earlier breeding experiments were concerned (Gerould, 1923), and attend to the measurable differences between the orange (red) and pure yellow exhibited in both sexes. Although we cannot measure the degree of redness or yellow carried latently by a white mother of a brood, we can measure the red and yellow averages of her sisters close to which her own "genotype" for these colors belongs. If she is an F_1 species-hybrid between *eurytheme* and *philodice*, that fact would be indicated also by her color pattern (dark border and other slight differences). The dominant gene for ♀-whiteness appears to be identical in the two species and may be introduced into the species-cross from either one of them. It has no influence upon the expression of the genes for orange or yellow recessive to it. Stocks free from this dominant gene are easily available, for in most regions white females (and males carrying the sex-controlled gene for female whiteness) are comparatively rare. At Hanover, N. H., only about 16 or 17 percent of the *philodice* females were found to be white.

The narrow, unspotted black border of the male *eurytheme* from Arizona is similar to that in *philodice*. In the female, however, the dark border of the hind wings is distinctly wider in *eurytheme* than in *philodice*, and broken along its inner edge with spots, an invasion of the ground color. In the female *philodice*, on the contrary, the marginal band on the hind wings is narrow or almost obsolete. Another, less clean-cut distinction between the two species is the fact that the central spot of the hind wing in *eurytheme* is deep orange; in *philodice* it varies from pale yellow to an orange less bright than in *eurytheme*.

Mating *eurytheme* with *philodice*

It has long been known that in the Mississippi Valley, where the faunal areas of the two species overlap, occasional matings between them occur. I have a pair of hybrids from a ♀ *eurytheme* caught *in coitu* with a *philodice* ♂ at Davenport, Iowa, by Mr. George Franck. At the Harvard Museum of Comparative Zoölogy (from Jos. Boll collection) is a group of three raised from the egg: "*Colias* hybrid, *eurytheme* ♂ × *philodice* ♀, Davenport, Iowa." It includes a pair, ♂ and ♀, evidently F_1 hybrids, and a paler orange ♂. Also, a ♂ from the A. G. Weeks collection ("Missouri, Aug. 9") and another ♂ from the H. C. Fall collection ("Oak Park, Chicago, July 8") are evidently F_1 hybrids.

Edwards (1868–1897, ser. 2) describes as a variety of *philodice* an orange-tinted ♂ from Illinois found paired with a yellow *philodice* ♀. His colored figure of this ♂ (*Colias*, pl. 3, fig. 1) is an excellent picture of an F_1 hybrid. Edwards refers to it by saying: "The yellow species may sometimes acquire characteristics of the orange without actual hybridism, according to the fact stated by Darwin (*Origin of Species*, 5th Am. Ed., p. 138) that 'the varieties of one species when they range into the habitations of other species often acquire in a slight degree some of their characters.'" But Edwards adds: "Or the present may be an example of hybridism, for that the orange species do sometimes mate with the yellow is not to be doubted."

Although the two are structurally much alike except for the pronounced difference in ground color and in the ♀ color pattern, I found a decided lack of cross-pairing affinity between the ♂ of *eurytheme* and the ♀ of *philodice* in some of the strains with which I experimented. Less difficulty in cross-mating was usual when the ♂ of *philodice* was used. Clark (1932: 159) observed a similar tendency in *philodice:* "The males of this species are very attentive to the smaller females of the orange clover (*Colias eurytheme*) though the orange males take little notice of the yellow females."

For the preliminary studies on *eurytheme* in 1912, a fertile female sent July 25 from Tempe, Arizona, to Harpswell, Maine, arrived July 31 and, set over red clover, laid a few eggs. From August 2 to 5 she laid abundantly. On September 10, for transportation to Hanover, N. H., 24 full-grown larvae were transferred to garden pea vines, which they ate well. The first pupation was September 12, the others September 14–17; eclosion September 25–29, as "1912u": 9 ♀ ♀ and 4 ♂ ♂ (all bright orange). This excess of females, later proved to be unusual, was con-

BROODS OF 1913

♀ = WHITE ♀. THIS CHARACTER, DOMINANT TO ORANGE-YELLOW AND PRESENT IN MOST OF THE WILD *EURYTHEME* STOCKS USED, IS TO BE DISREGARDED IN THE PRESENT PAPER WHICH DEALS ONLY WITH COLORS OF THE ♂ AND OF THE ORANGE OR YELLOW ♀.

BROOD	SPECIES OR RACE	PARENTS	FIRST AND LAST MEMBERS	TIME OF ECLOSION	TOTAL IMAGINES	♂♂	♀♀	♀♀	IMMEDIATE DESCENDANTS
a	*EURYTHEME*	WILD ♀ "A" FROM ARIZONA	a^1 ♂ – a^{111} ♂	JULY 6 – 29	111	57 AND 1 GYNANDER	24	29	d (*EURY.*), e (*EURY.*) AND p(F_1)
d	*EURYTHEME*	a^{19} ♀ x a^{39} ♂	d^1 ♀ – d^{12} ♂	AUG. 24 – SEPT. 22	12	4	4	4	t (BACKCROSS TO *EURY.*)
e	*EURYTHEME*	a^{59} ♀ x a^{27} ♂	e^1 ♂ – e^{24} ♀	SEPT. 7 – OCT. 3	24	15	0	9	u (BACKCROSS TO *EURY.*)
p	F_1 HYBRIDS	a^{94} ♀ x WILD *PHIL.* ♂	p^1 ♀ – p^{18} ♂	AUG. 28 – SEPT. 22	18	11	3	4	q(F_2), s (BACKCROSS TO *EURY.*)
b	*EURYTHEME*	WILD ♀ "B" FROM ARIZONA	b^1 ♀ – b^{98} ♀	JULY 14 – 29	96	49	20	27	m(*EURY.*) o(F_1)
o	F_1 HYBRIDS	b^{78} ♀ x *PHIL.* ♂ FROM N.H.	o^1 ♀ – o^{143} ♂	AUG. 24 – SEPT. 19	143	72	35	36	q(F_2), r (BACKCROSS TO *EURY.*), t (BACKCROSS TO *EURY.*), u (BACKCROSS TO *EURY.*)
c	*EURYTHEME*	WILD ♀ "C" FROM ARIZONA	c^1 ♂ – c^{425} ♀	JULY 13 – AUG. 34	420	214	206	0	ONE CROSSMATING WITH *PHIL.* ♂ BUT DISEASE KILLED OFFSPRING
m	*EURYTHEME*	b^{53} ♀ x b^{48} ♂	m^1 ♂ – m^{65} ♂	AUG. 28 – SEPT. 27	65	38	11	16	r, s (BACKCROSS TO *EURY.*), v (F_1)
q	F_2	p^{11} ♀ x o^{10} ♂	q^1 ♂ – q^{19} ♂	NOV. 12 – 24	19	13	3	3	
r	BACKCROSS TO *EURY.*	m^{28} ♀ x o^{112} ♂	r^1 ♀ – r^{12} ♀	NOV. 14 – DEC. 11	12	5	7	0	
s	BACKCROSS TO *EURY.*	m^{26} ♀ x p^{15} ♂	s^1 ♂ – s^{181} ♀	NOV. 18 – 26	181	108	38	35	
t	BACKCROSS TO *EURY.*	d^5 ♀ x o^{124} ♂	t^1 ♀ – t^{72} ♂	NOV. 19 – 20	72	33	0	39	
u	BACKCROSS TO *EURY.*	e^{10} ♀ x o^{132} ♂	u^1 ♂ – u^{64} ♀	DEC. 4 – JAN. 10	64	36	13	15	
v	F_1	m^{18} ♀ x *PHIL.* ♂	v^1 ♂ – v^{33} ♂	NOV. 26 – DEC. 11	33	25	5	3	ALSO MORE THAN 353 PUPAE OF THIS BROOD UNDERWENT PARTIAL HIBERNATION.

BROODS OF 1914

♀ = WHITE ♀

BROOD	SPECIES OR RACE	PARENTS	FIRST AND LAST MEMBERS NUMBERED	TIME OF ECLOSION	TOTAL	♂♂	♀♀	♀♀	IMMEDIATE DESCENDANTS
x	*EURYTHEME*	X ♀ (ARIZONA) WILD ORANGE	x^1 ♂ – x^{90} ♂	JULY 8 – 20	285	149	136	0	a(F_1)
y	*EURYTHEME*	Y ♀ (ARIZONA) WILD WHITE	y^1 ♂ – y^{55} ♀	JULY 10 – 21	57	29	15	13	c(F_1), d(F_1)
z	*PHILODICE*	Z ♀ (N.H.) WILD YELLOW	z^1 ♂ – z^{87} ♀	JULY 11 – 24	88	47	41	0	a(F_1), c (F_1), d(F_1)
a	F_1	z^{40} ♀ x x^{63} ♂	a^1 ♂ – a^{162} ♀	AUG. 16 – SEPT. 9	162	122	40	0	e (F_2), g (F_2), h (BACKCROSS TO *PHIL.*)
e	F_2	a^{101} ♀ x a^{102} ♂	e^1 ♀ – e^{12} ♂	OCT. 13 – 29	12	6	6	0	
f	F_2	a^{98} ♀ x a^{105} ♂	———	———	2	1	1	0	
g	F_2	a^{103} ♀ x a^{104} ♂	g^1 ♀ – g^{32} ♂	OCT. 10 – 31	34	22	12	0	
h	BACKCROSS TO *PHIL.*	a^{129} ♀ x WILD *PHIL.* ♂	h^1 ♂ – h^{60} ♂	OCT. 14 – DEC. 15	60	24	36	0	
i	F_3	h^7 ♀ x h^3 ♂ BOTH PALE HETEROZYGOTES	i^1 ♂ – i^{22} ♂	NOV. 29 – DEC. 15	22	13	9	0	
c	F_1	z^{26} ♀ x y^{41} ♂ *PHIL.* *EURY.*	c^1 ♂ – c^{81} ♀	AUG. 17 – 27	61	45	9	7	(PRESENCE OF 7 ♀♀ DUE TO ♂ y^{41} ALONE. z^{26} ♀ WAS RECESSIVE FOR DOMINANT ♀-WHITENESS.)
d	F_1	y^{44} ♀ x z^{13} ♂	d^1 ♀ – d^{54} ♂	SEPT. 1 – 13	54	20	10	24	(STRANGE EXCESS OF ♀♀ DUE TO y^{44} ♀ ALONE.)
b	F_1	z^{38} ♀ x x^{69} ♂	b^1 ♂ – b^6 ♂	———	6	6	0	0	

FIG. 1. Broods of 1913 and 1914.

tinued in the F_1 (*eurytheme* ♀ × *philodice* ♂) hybrids.

All of the 9 *eurytheme*, 1912u, females mated: 4 with 2 of the *eurytheme* males (the other 2 males not mating); 5 mated readily with 5 wild *philodice* males. Three of the *eurytheme inter se* matings were fertile; one female laid sterile eggs.

Of the 5 matings with *philodice* males, one was sterile, the others produced, early in December, a few almost exclusively female offspring:

u^9 ♀ produced 1912a, 11 ♀ ♀ + 1 ♂ (Nov. 29–Dec. 5, eclosion)
u^7 ♀ produced 1912b, 4 ♀ ♀ + 1 ♂ (Dec. 1–7)
u^5 ♀ produced 1912c, 3 ♀ ♀ (Dec. 7)
u^1 ♀ produced 1912d, 1 ♀ (Dec. 8)

All members of these fragmentary F_1 broods were small and faintly orange (except 3 white females of "b," due to the gene for ♀-whiteness introduced by the wild *philodice* mate). If caught wild, they would probably have been called "*ariadne*" by collectors. Measurements of the faintly orange tints of the 11 ♀ ♀ of 1912a are shown in figure 2.

In 1913, *philodice* not being abundant, no virgin *philodice* females were available. As in 1912, the cross-matings were: *eurytheme* ♀ × *philodice* ♂. Four such matings occurred from which the F_1 broods 1913o, p, v (fig. 1) were raised. Twenty-five selfed matings were made in 1913 within the three *eurytheme* stocks of that year (fig. 1): 11 in 1913a, 7 each in 1913b and 1913c. (The same brood letters "a"–"d," designating F_1 hybrids in 1912 and 1914, were applied in 1913 to broods of pure *eurytheme*.)

The reciprocal cross, *philodice* ♀ × *eurytheme* ♂, received particular attention in 1914 (fig. 1), and 4 matings were obtained, giving F_1 families 1914a, b, c, the 4th not being reared, while the combination with a *philodice* ♂ also occurred 4 times; one made July 14 gave family d.

In general, interspecific matings involving the *philodice* ♂ were more readily obtained than the reciprocal combination, which, however, sometimes occurs and is fertile.

Extensive mating experiments were made in 1914 to test pairing affinity in reciprocal species-crosses in comparison with that between individuals within either one of them. On July 18 I tried all the afternoon to get matings between 19 *philodice* ♀ ♀ and 33 *eurytheme* ♂ ♂ and, simultaneously, between 25 *eurytheme* ♀ ♀ and 11 *philodice* ♂ ♂ in another cage. No mating occurred in either cage. At 3:30 p. m., however, a *philodice* ♀ (melanic aberration) was transferred to the cage in which the 11 *philodice* ♂ ♂ were flying. An hour later she mated within her species.

On July 20, between 1:30 and 6 p. m., in an attempt to secure matings between 23 *philodice* ♀ ♀ and about 40 *eurytheme* ♂ ♂, only one mating occurred (z^{40} ♀ × x^{63} ♂, parents of 1914a—see fig. 1). Yet when 4 of these *eurytheme* ♂ ♂, after flying two hours with ♀ ♀ of the other species without mating, were transferred to a cage with 10 *eurytheme* ♀ ♀, three of them soon mated. Pairing affinity within *eurytheme* was excellent. Again on July 22, 40 *eurytheme* ♂ ♂ flew for three hours with 21 *philodice* ♀ ♀ and no mating occurred. But on the same afternoon 13 *eurytheme* ♂ ♂ and 13 *philodice* ♂ ♂ were caged with 13 *eurytheme* ♀ ♀. Four matings resulted: one being a pair of *eurytheme*, three a *eurytheme* ♀ × *philodice* ♂ cross.

The F_1 broods were in most cases of considerable size. They were:

eurytheme ♀ × *philodice* ♂: 1913o, 143 adults; 1913p, 18 adults; 1913v, 33 adults (+ 353 pupae); 1914d, 54 adults
philodice ♀ × *eurytheme* ♂: 1914a, 162 adults; 1914b, 6 adults; 1914c, 61 adults

Mating of the Hybrids, and Sterility

F_1 hybrids between *eurytheme* and *philodice*, by either of the reciprocal crosses, mated together readily. But whereas in 1913 8 out of 9 of these F_1 unions proved sterile when a *philodice* ♂ had been the original ♂ parent, none was completely sterile when in 1914 a *eurytheme* ♂ had been. Yet, as has been shown, cross-pairing with the *eurytheme* ♂ was less readily accomplished, sexual affinity apparently being lacking. Thus the two species seem to be separated by two barriers. When mating was readily accomplished (*philodice* ♂), the hybrid offspring were in most cases sterile when mated *inter se;* the reciprocal cross, commonly prevented by lack of sexual attraction, resulted in only slightly fertile F_1 offspring. The following notes support this conclusion.

In 1913 I mated 9 pairs of F_1 hybrids from the original cross *eurytheme* ♀ × *philodice* ♂. The matings were in every way normal, lasting over 1½ hours. Only one ♀ laid fertile eggs (p^{11} ♀ × o^{10} ♂ = q); this was the only F_2 species-hybrid brood raised in 1913 and it included only 19 adults. Another F_1 ♀ (o^{37}), mated with

o^{16} ♂, was kept nearly a month (September 5 to October 2) over a clover plant, and having laid no eggs was dissected. The ovaries were perfectly developed, and in the vagina was one red egg (the color usually assumed by eggs several hours after laying); the oviducts were full of large, fully-developed eggs. The presumption is, therefore, that the F_1 ♂ mate, o^{16}, rather than the ♀, was sterile.

A second F_1 ♂, o^{13}, is to be regarded as sterile because neither of his two sisters nor the *eurytheme* ♀, with all of which he mated, laid any eggs. A third F_1 ♂, o^9, was backcrossed to *eurytheme*, m^{40} ♀, with no offspring. Which mate was sterile is uncertain.

On the other hand, four F_1 ♂♂ backcrossed to *eurytheme* were fertile, producing broods r, u, t, and s, with 12, 64, 72, and 181 offspring. The limited productivity in "r" may be due to the ♂, o^{112}, since he had no offspring by another *eurytheme* ♀, d^1.

In brief, 5 of the F_1 ♂♂ in 1913 were fertile, 2 were sterile. One F_1 ♀ (p^{11}) was fertile but produced only 19 offspring. Another F_1 ♀, o^{37}, apparently was fertile but had a sterile mate, o^{16}. In four sterile F_1 *inter se* matings and one *eurytheme* backcross, it is uncertain which sex was sterile.

Within *eurytheme* of 1913 there were nine fertile and only five sterile matings, two of the latter involving the same male. On the other hand, only one of the nine $F_1 \times F_1$ matings was fertile, with only 19 adult offspring.

In August, 1914, numerous *inter se* matings (3 on August 26; 10 on August 31, when others easily could have been obtained) between the F_1 hybrids from the original cross *philodice* ♀ × *eurytheme* ♂ were quickly made, in marked contrast to the difficulty experienced in making the original cross. In only a few cases were the fecundated F_1 ♀♀ tested for egg-laying. These proved slightly fertile but not at all prolific (brother-sister matings producing F_2 families: e, f, g, 12, 2, 34 imagines). The backcross with *philodice* ♂ (1914h) and the latter inbred (1914i) were also fertile.

The three F_2 broods were all small. One of them, 1914e, consisted of only 12 imagines; the mother (a^{101}) laid a few eggs on August 30, and many on September 1; but the last, laid between September 27 and October 9 (when the ♀ was killed) were sterile. Brood f (from a^{98} ♀ × a^{105} ♂) was attacked by disease; only two imagines survived. Brood g (from a^{103} ♀ × a^{104} ♂) was larger, 34, but small compared with the backcross with *philodice* (1914h, 60 imagines) and the still larger backcrosses with *eurytheme* (1913s = 181, t = 72, u = 64).

Inheritance of Orange Wing-Color in F_1

Red (orange) in F_1 species-hybrids between the orange-yellow *eurytheme* and the clear yellow *philodice* is incompletely dominant. Even in midsummer, when the hybrid's colors as well as those of *eurytheme* are strongest, the orange wing-color of the hybrid is much less intense than in *eurytheme*, which at this season is sometimes called "*amphidusa*," if strongly colored, or "*keewaydin*" if slightly less so. Although the F_1 color is much less variable than that of the spring (or winter) seasonal variety, the diminutive "*ariadne*," its intensity in red is comparable to that.

No red was visible by ordinary inspection in the *philodice* stock used in cross-breeding. In measuring with the Levibond colorimeter the posterior part of the upper surface ("inner" margin) of the forewing (the region regularly chosen because orange is there most constant in *eurytheme*), *philodice* showed only a trace of red, well below 1.0. For example, in 1910k the average of red in 32 ♂♂ was 0.26 ± .01; in 16 ♀♀, 0.3 ± .01; in 1910e (fig. 2), 24 ♂♂ gave an average of 0.30 ± .03; 13 ♀♀, 0.62 ± .02. These emerged in August. A July brood, 1914z, showed a larger red component than those just mentioned but less than 1.0. The 29 ♂♂ gave an average measurement of 0.78 ± .02; 14 ♀♀, 0.87 ± .01.

Contrast these with the high averages in *eurytheme* in summer (fig. 2):

1913b (July eclosion): 49 ♂♂ gave an average in red of 3.99 ± .09; 19 ♀♀ gave an average in red of 3.56 ± .14

1913m (September): 24 ♂♂ gave an average in red of 4.23 ± .10; 8 ♀♀ gave an average in red of 3.81 ± 2.0

The yellow of *philodice* is approximately "picric yellow" (Ridgway, 1912), which with the Levibond instrument measured 0.4 red. By Ridgway standards, the summer *eurytheme* is roughly "cadmium yellow," 4.7 red, Levibond. The reduced orange, or intermediate coloration, of the F_1 summer species-hybrid is approximately "apricot yellow" of Ridgway, 2.75 Levibond, but varies between "empire yellow," 1.8 Levibond,

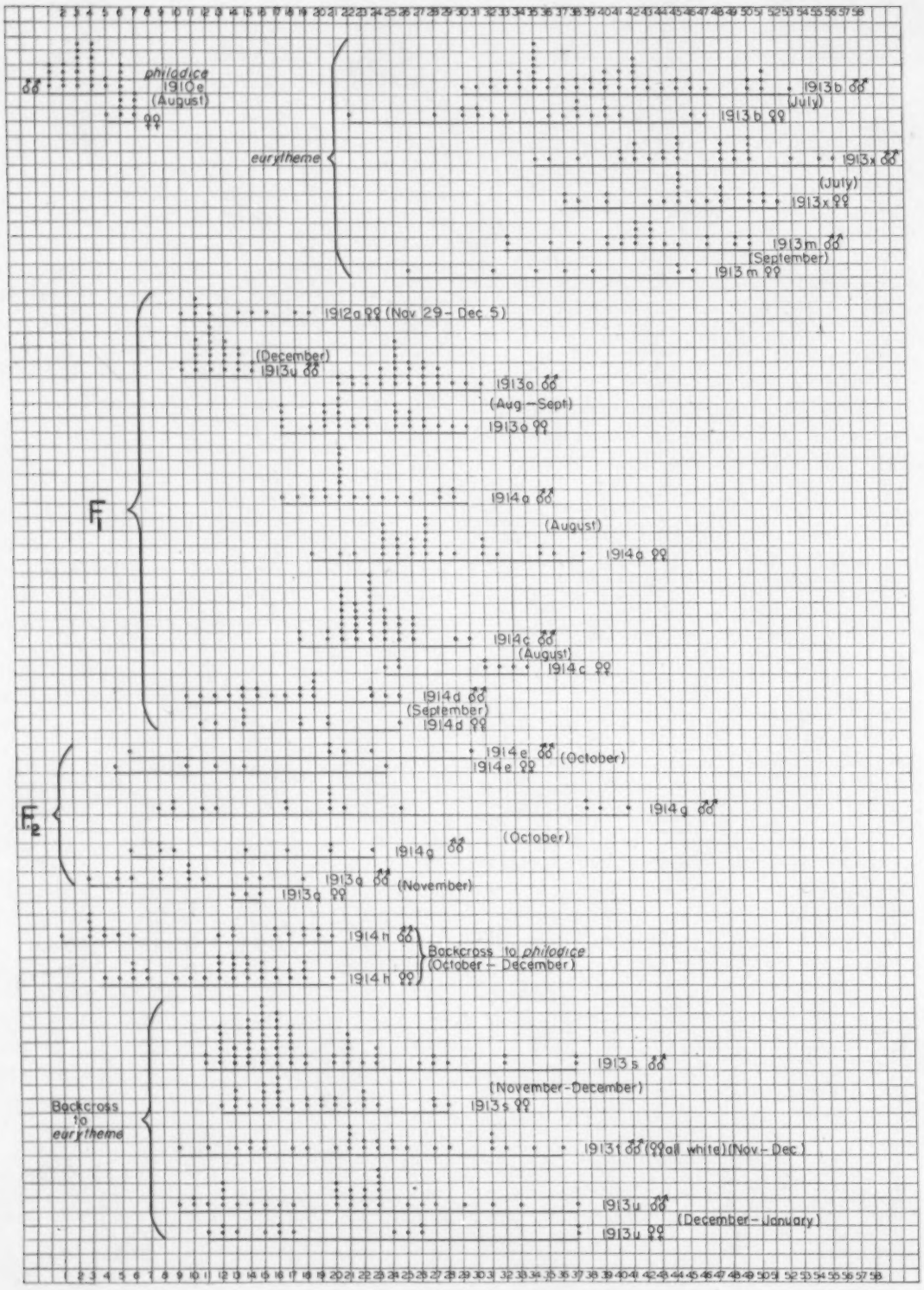

FIG. 2. Sample measurements in Levibond units of red × 10 of broods of *C. philodice*, *C. eurytheme*, and hybrids, with dates of emergence of each brood. The *C. eurytheme* stock was from Arizona, *C. philodice* from New Hampshire. Each dot shows the maximum red on a forewing of a single butterfly.

and "light cadmium," 3.2 Levibond. More precisely, the F_1 range for August ran from 1.7 to 3.8 Levibond.

That averages in red of summer F_1 broods, except in certain ♀ ♀, were slightly less (paler) than "apricot yellow," 2.75, is shown by the following table:

AVERAGES OF RED IN F_1 HYBRIDS (SUMMER)

Brood	Males	Number measured	Females	Number measured
1913o	2.55±.05	29	2.30±.06	29
1914a	2.22±.07	25	2.74±.08	30
1914c	2.30±.04	42	2.90±.13	9

These summer F_1 averages, it will be observed, show a numerical drop from the *eurytheme* summer averages by about one-third (slightly more than one-third in the males, slightly less than that in the females).

The intensity of red in F_1 being much reduced from that of pure *eurytheme*, the range of its variation in F_1 was correspondingly less. The average range in *eurytheme* was about 2.0; in four F_1 broods it was only 1.3, as shown by the following table and figure 2.

RANGE OF RED IN *eurytheme*

			n
1913b	♂♂	5.3–3.0 = 2.3	49
	♀ ♀	4.7–2.2 = 2.5	19
1913m	♂♂	5.0–3.2 = 1.8	24
	♀ ♀	4.6–2.6 = 2.0	8
1914x	♂♂	5.6–3.5 = 2.1	26
	♀ ♀	5.2–3.7 = 1.5	22

Average range 2.0

RANGE OF RED IN F_1

			n
1913o	♂♂	3.1–2.1 = 1.0	29
	♀ ♀	3.0–1.8 = 1.2	29
1914a	♂♂	3.0–1.7 = 1.3	25
	♀ ♀	3.8–1.9 = 1.9	30
1914c	♂♂	3.0–1.8 = 1.2	42
	♀ ♀	3.4–2.4 = 1.0	9
1914d	♂♂	2.5–1.0 = 1.5	20
	♀ ♀	2.5–1.1 = 1.4	10

Average range 1.3

Seasonal effect on F_1.—Two other F_1 broods show a pronounced inhibitory seasonal effect on development of red, viz, 1914d and 1913v (fig. 2).

The former came from a white *eurytheme* mother (y^{44}), whose orange sisters had a red average of 4.76 ± .10, the brothers 4.79 ± .07 (eclosion July 11–14). The *philodice* father (z^{13}) measured 0.9 in red. The F_1 hybrid ♂ offspring had a red average of only 1.7 ± .10, ranging from 1.0 (slightest tinge of red) to 2.5 (pale orange) (20 ♂♂ measured).

That temperature alone was responsible for this low average in red, as compared with the F_1 broods raised less than a month earlier in the greenhouse, seems unlikely. The facts are these: the larvae of 1914d fed entirely outdoors during the first 3 weeks of August when the official temperature at Hanover was 69.1° F., 2.3° higher than the July average of that year (66.8°) and 1.3° above the August normal. The pupae, however, were exposed to two cold nights, August 24 and 25, when the official temperature was 42.9° F. (6° C.) and 39° F. (3.9° C.), and they were brought into a steadily cool basement room (temp. about 65° F. or 18° C.). Eclosion occurred September 1–13.

It is evident that temperatures to which the larvae were exposed did not produce the obviously lowered intensity of orange, and, in view of other facts to be brought out in a later section (p. 418), it seems unlikely that the exposure of the pupae to the two somewhat cold nights (6° C. and 3.9° C.) produced this effect, though the exposure came at the time of pupation, a period which has come to be regarded as critical for wing-pigment development in diurnal Lepidoptera.

The other F_1 brood, 1913v, mentioned above and in figure 2, shows still better the seasonal effect. The mother, a white *eurytheme* (m^{12}) had been mated to a *philodice* ♂ on September 9. She was not given opportunity to lay until September 27 and 28, when she laid profusely outdoors. Hatching began October 5; pupation, October 27.[1]

All the 34 imagines constituting 1913v came from larvae which pupated November 16–20; they emerged November 26–December 6. During the first two weeks of November and the very last of October the larvae fed on clover which was brought into the greenhouse after heavy frosts and was less succulent than in summer.

[1] More than 350 chrysalids from the first of these eggs were put into a fairly moist, cool cellar. They died, mostly during February. A few which were allowed to mature in the greenhouse between February 28 and March 6 emerged imperfectly; they were unable to extract from the pupa-case their desiccated abdomens. Hibernation of half-grown caterpillars is the rule in these species; such caterpillars survive the natural winter dehydration which is fatal to most of the pupae.

The pupae were exposed only to normal room temperature, November 16–26.

The range in red in 1913v extends only from 1.0 to 1.5 in 25 ♂♂ (fig. 2), and from 1.0 to 1.2 in 5 ♀♀, with an average of 1.24 ± .03 in the ♂♂. The *philodice* parent measured 0.8 in red; the red average of the sisters of the white mother, m^{12}, was 3.8 ± .25 (eclosion September 2–20). The orange of these F_1 winter hybrids is limited to the forewings and to a faint patch extending from the center to the posterior margin of the wing; in most cases it is merely a delicate flush of color between the cubitus veins and behind the anal vein. Three of the 30 non-white individuals show by ordinary inspection no trace of orange (excepting the dominant brilliant discal spot of the hind wing).

The most remarkable feature of this winter or late fall F_1 brood, 1913v, was the narrow range of variation in red, only 0.5 for the 25 individuals. In the September F_1 brood, 1914d, it was 1.5, covering the extremely narrow range of 1913v and extending over the lower half of the ranges of the F_1 summer broods.

F_2 of the Species-Cross

Indications of segregation are best seen in the wide range of variation in the 17 males of the largest of the three small F_2 broods which came through to maturity, viz, 1914g (pl. A; figs. 2 and 3). This range amounts to 3.3, extending from that of the moderately brilliant autumn orange form (*"keewaydin"*), 4.1, into clear yellow, 0.8. This wide range is nearly three times that of any F_1 brood. There is a distinct gap between the four bright orange males (two at 3.8, one each at 3.9 and 4.1) and the eight intermediates, which form an isolated group between 2.5 and 1.7, the largest number (4) measuring 2.0 like the two F_1 parents. At the bottom of the scale there are five yellow males. Three of these fall below 1.0, two (1.15 and 1.2) barely above it but distinctly below the palest orange heterozygote (1.7).

The 11 ♀♀ show less variation, a range of only 1.7. The brightest ♀ measures in red only 2.3, scarcely brighter in red than the F_1 parents, but there is a clearly visible gap between the palest heterozygote (1.4) and the yellows, which measure less than 1.0.

Another F_2 brood, 1914e, though very small (6 ♂♂, 5 ♀♀), shows a range in the male of 2.4 (fig. 2), or about twice that of the summer F_1 and

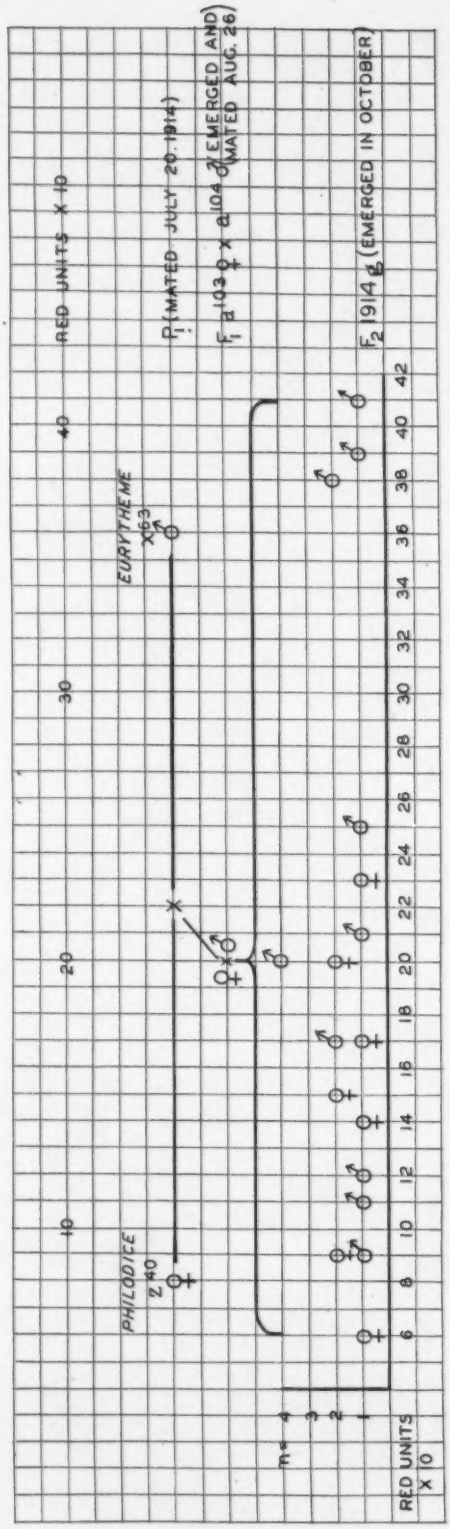
RED UNITS X 10
RED UNITS X 10
PHILODICE
EURYTHEME
P1 (MATED JULY 20, 1914)
F1 ♂103 ♀ X ♂104 ♂ (EMERGED AND MATED AUG. 26)
F2 1914 g (EMERGED IN OCTOBER)
m=4
3
2
1
6 8 10 12 14 16 18 20 22 24 26 28 30 32 34 36 38 40 42

FIG. 3. Measurements in red units × 10 of the three generations shown in plate A. Abscissas represent the color range; ordinates the number (*n*) of individuals of each sex with the respective degrees of redness. The original orange male (x^{63}) stands low (36 red units) in its brood, 1914x, which extends upward to 56 red units (fig. 2). It was the 63rd in its brood to emerge.

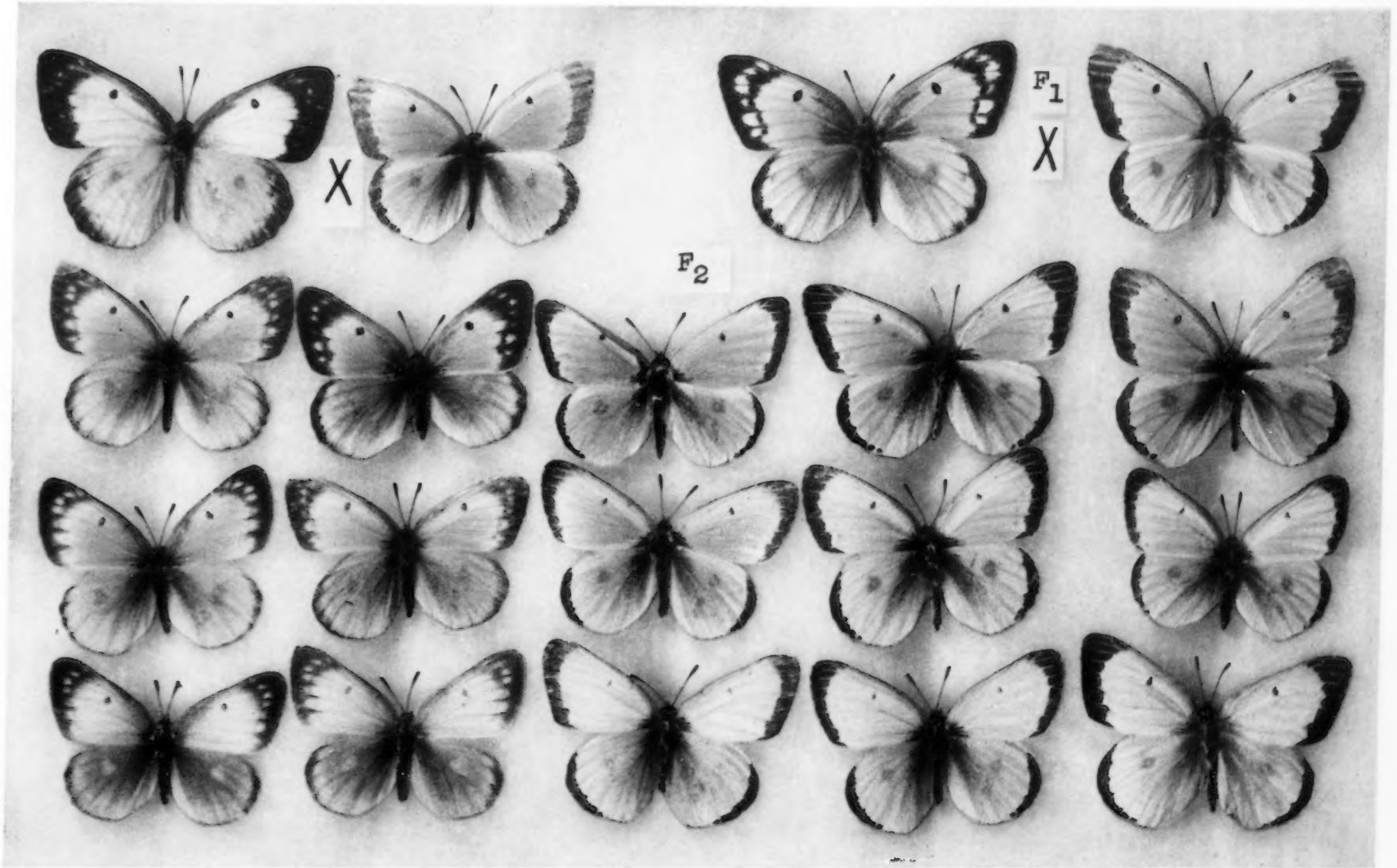

PLATE A. *C. philodice* ♀ × *C. eurytheme* ♂ (upper left). F_1 pair, 1914 a, August.
F_2 : 1914 g (October), 6 females on left, 9 males on right.
(A fresh, but nearly identical, sister is shown in place of each very dilapidated mother)

slightly greater than that of the most variable brood of summer *eurytheme*. These ♂♂ are in two distinct groups. Five are orange (two at 2.0 and one each at 2.1, 2.3, and 3.0), with a very wide gap between them and the single yellow ♂ at 0.6. Of the five measured ♀♀, only one is decidedly orange (2.4), but even that falls below the ♀ F_1 parent (2.7); two are extremely pale orange (1.2 and 1.4); and two are distinctly yellow (0.5 and 1.0). The range in the females, 1.9, does not exceed that of an F_1 brood.

A third F_2 brood, 1913q, which emerged November 12–24, includes 13 ♂♂ and 3 non-white ♀♀ (fig. 2). By simple inspection, 10 of the ♂♂ were recorded as orange, 3 as yellow. In Levibond red units, the latter measure only 0.3 and 0.5. Three faintly orange ♂♂, as viewed by simple inspection, fall below 1.0, which in most broods is about the minimum of distinctly visible orange. Their values in red were 0.6, 0.8, and 0.8. Three other faintly orange ♂♂ measured 1.0, and another 1.1. A slight break occurs between the three highest in red (1.3, 1.4, and 1.8), which we may regard as homozygous, and the seven heterozygotes, but no gap occurs between the visibly faint orange and clear yellow. The range of red in 1913q, 1.5, is hardly more than that of the summer F_1 males (1.0, 1.2, 1.3). Seasonal reduction in orange is shown by comparing the F_1 male parent, 2.1 in red, with the brightest F_2 son, 1.8 in red. Eclosion of the three brightest individuals in 1913q, November 12–18, was exactly a month later than that of the four brightest in the F_2 brood, 1914g, which largely explains the failure of 1913q to produce any strongly orange individuals.

Although orange variations in members of these three broods grade into clear yellow in almost continuous series, it is possible by simple inspection to distinguish those which are visibly pure yellow from those which show a faint flush of orange suffused upon the yellow background. In other words, segregation is evident in the F_2 not only by its wider range of variation than that of F_1, as observed in the male, but also by the partial separation into two classes, as follows:

		Orange	Yellow
1913q	17 individuals	13 (10 ♂♂, 3 ♀♀)	4 ♂♂ (+3 white ♀♀)
1914e	12 "	9 (5 ♂♂, 4 ♀♀)	3 (1 ♂, 2 ♀♀)
1914g	32 "	24 (17 ♂♂, 7 ♀♀)	10 (5 ♂♂, 5 ♀♀)
	Total	46 orange	17 yellow
Expectation on basis of 1 pair of genes		47.25	15.75

Orange in *C. eurytheme* is a character so subject to seasonal changes that late fall and winter conditions, to be discussed later, uniformly reduce the intensity of orange throughout the whole series of a highly variable F_2 brood. The result is a color scale at a lower pitch, as it were, but with corresponding intervals. In other words, we find that the most highly colored homozygous members (about 25 percent) of an F_2 brood raised in October and November are paler than summer F_1 hybrids and are "*ariadne*"-like, while the individuals of corresponding families raised a month earlier (September–October) are more brilliant and "*keewaydin*"-like. From both of them an almost unbroken descending scale of color intensity in the heterozygotes occurs, ending in some in which the orange pigment is barely visible. It is accordingly reasonable to assume that late fall conditions acting on such a brood as this, bred under as nearly uniform conditions as can be obtained in a greenhouse, with potted foodplants, affect the production of such a continuous series of orange variations by reducing all equally.

Backcross of F_1 to the Recessive *philodice*

The single brood, 1914h (pl. B), of this important combination emerged from October 14 to December 15. Accordingly it shows a seasonal reduction in redness in that part of it consisting of orange heterozygotes, none of which are brighter in red than 2.0 (fig. 2). This upper limit of the orange heterozygotes is exceeded in redness by almost all of the summer F_1 individuals. A few of an autumn F_1 brood, 1913d, measuring 2.3–2.5, also exceed it.

The males of this backcross fall naturally into two very distinct groups, 9 yellow recessives, equivalent in ground color to *philodice*, and 11 orange heterozygotes; there is a wide interval of 0.6 between these two groups. The *philodice*-like individuals cluster around 0.3 (like the ♂ parent, 0.4); the orange heterozygotes vary between 1.2 (faintly orange) and 2.0, identical with redness of the heterozygous mother.

The 33 females include a recessive yellow group of only 9 and nearly three times as many (24) pale orange heterozygotes, distributed within the same limits as the males but concentrated at lower (paler) levels. Segregation into orange heterozygotes and yellow recessives gives in both sexes a distinctly bimodal curve.

The disparity in number between the yellow cf. orange in the females, when equality, as in

the males, would be expected on a unifactorial basis, may be attributed to mere chance in view of the small numbers. No lethal factor eliminating a half or more genotypically yellow ♀♀ is to be expected.

Seasonal effect on redness in 1914h (October–December) is seen in the fact that the brightest orange ♀ measures only 2.0 (fig. 2), which is nearly identical with the palest orange ♀ of the (summer) brood of the heterozygous mother (1914a, August eclosion), and 0.7 below the ♀ average and 1.8 below the brightest orange ♀, 3.8, of that brood. Likewise, the 6 brightest orange males of 1914h equal only the palest males of the mother's brood.

A notable feature of this backcross family is almost complete agreement between the color of the discal spot of the hind wing and the ground color (pl. B). The yellow father of the brood, a male *philodice*, had a yellow discal spot. Orange is invariably the case in *eurytheme* and sometimes occurs in the *philodice* female. All the offspring that are even faintly orange in this brood have also an orange discal spot; all those with yellow ground color have a yellow discal spot.

Backcross to *eurytheme*

The backcrosses of F_1 females to *eurytheme* males (1913s, t, u, fig. 2) show inhibiting seasonal effects on orange coloration; all emerged in November–December (into January in one case) in greenhouse cultures.

The range of variation extends upward into red through merely the lower part of *eurytheme*'s summer range, viz., to 3.7. This point is at or near *eurytheme*'s ♀ summer average (1913m, 3.8; 1913b, 3.56) and is slightly below the summer average of the ♂. The paler end of this backcross range extends beyond the entire narrow range of the winter (December) F_1 (1913v, 1.0 to 1.5) and even slightly below the lowest limits of easily visible redness, viz, to 0.9. Roughly 11 percent of 1913s (exclusive of white ♀♀) would be classed as the moderately orange "*keewaydin*," and about 25 percent of the brood probably would be regarded as the pale orange "*ariadne*." Between the two is a continuous series of intermediate grades.

At the lowest limits there are a few individuals (in 1913t and u) in which by ordinary inspection no orange is visible. They measure in redness 0.9 and 1.0. Similar pure yellow specimens occur in F_1 winter hybrids (3 in 31 in 1913v, 2 ♂♂ and 1 ♀). These backcross yellows are obviously not extracted recessives, but heterozygotes held back in color development by seasonal conditions.

One backcross brood, 1913s (fig. 2), gives skew curves in both sexes, with most of the individuals concentrated near the yellow end of the range. Another, 1913u, shows a slight tendency toward two modes.

The averages for red in each of these winter backcross broods (1913s: ♂♂ = 1.77 ± .07, ♀♀ = 1.8 ± .08; 1913t: ♂♂ = 2.2 ± .13; 1913u: ♂♂ = 2.0 ± .11, ♀♀ = 2.05 ± .24) is slightly below those of the summer F_1 (1913o: ♂♂ = 2.56 ± .05, ♀♀ = 2.30 ± .06; 1914c: ♂♂ = 2.3 ± .04, ♀♀ = 2.9 ± .13; 1914a: ♂♂ = 2.22 ± 1.3, ♀♀ = 2.74 ± 1.9).

Under summer conditions, such backcross averages for red would be expected to lie halfway between the summer average for F_1, 2.4, and the average for pure *eurytheme*, 4.0 (*i. e.* about 3.2); actually the average did not exceed 2.2.

Coefficients of Variability

Through the kindness, initiative, and mathematical skill of Dr. James Franklin Crow the following measurements of variability in the various 1913 and 1914 broods have been computed.

Comparing the combined coefficients of variability in redness of three broods of Arizona *eurytheme* (1913b, m, and x) with three of the *eurytheme–philodice* F_1 (1913o, 1914a and c), we find F_1 only slightly less variable than *eurytheme*. In the males of *eurytheme* the average percent was 12.7, vs. 12.2 percent in F_1. In the slightly more variable females, the 15.36 percent in *eurytheme* was reduced in F_1 to 15.0 percent.

In F_2, however, the coefficients of variability were enormously increased over those of F_1. The males of three broods gave an average of 46.1; in the females of two broods (excluding one of only two individuals) the average percent was 47.1.

In the backcross to *philodice* (1914h), the coefficient in the male was 65.2 percent, even greater than in F_2, while in the female it was 37.7 percent.

Combining the coefficients of the three F_1 × *eurytheme* backcrosses, we find averages of 32.4 percent for males, 33.5 percent for females.

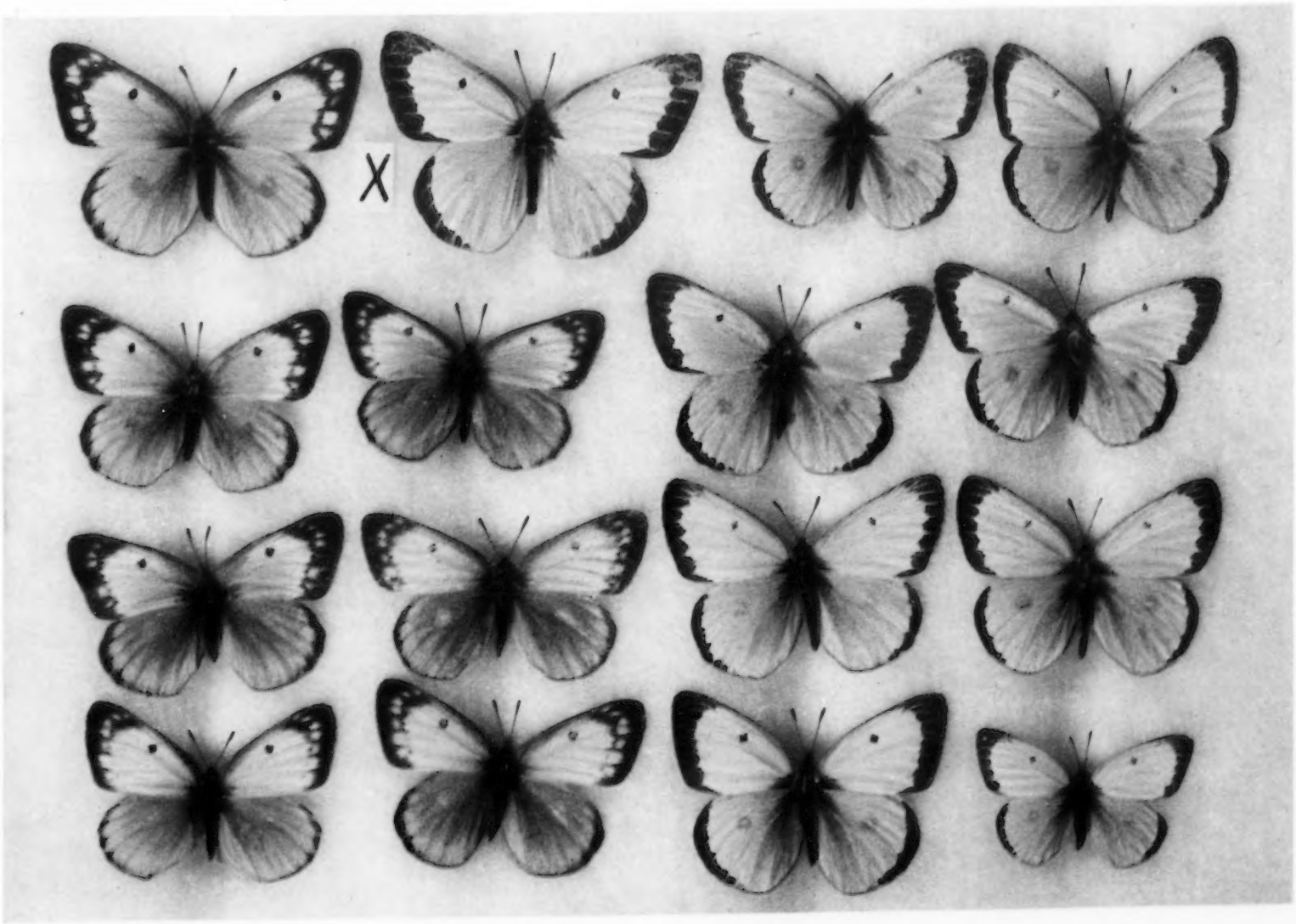

PLATE B. Backcross : F_1 ♀ (of 1914 a) × philodice ♂ (upper left).
Offspring (late fall, 1914 h) : 6 females on left (3 pale-orange, 3 yellow), 8 males on right (4 pale-orange, 4 yellow).

TABLE 1

MEASUREMENTS OF SAMPLES OF VARIOUS BROODS IN BASIC RED UNITS (NOT × 10)

	Brood	N	Mean	Range	Standard deviation	Coefficient of variation in percent
Philodice	♂ Aug. 1910e	24	.30 ± .03	.4	.12 ± .02	42.6 ± 7.2
	♀	13	.62 ± .02	.2	.07 ± .01	10.9 ± 2.2
	♂ Aug. 1910k	32	.26 ± .01	.1	.05 ± .01	19.8 ± 2.6
	♀	16	.30 ± .01	.2	.05 ± .01	17.2 ± 3.1
	♂ July 1914z	29	.78 ± .02	.2	.08 ± .01	10.3 ± 1.4
	♀	14	.87 ± .01	.1	.05 ± .01	5.5 ± 1.1
Eurytheme	♂ July 1913b	49	3.99 ± .09	2.3	.60 ± .06	15.0 ± 1.5
	♀	19	3.56 ± .14	2.5	.63 ± .10	17.5 ± 2.9
	♂ July 1914x	26	4.59 ± .10	2.1	.52 ± .07	11.4 ± 1.6
	♀	22	4.52 ± .10	1.5	.45 ± .07	10.0 ± 1.5
	♂ Sept. 1913m	24	4.23 ± .10	1.8	.50 ± .07	11.7 ± 1.7
	♀	8	3.81 ± .25	2.0	.71 ± .18	18.6 ± 4.8
	♂ July 1914y	23	4.79 ± .07	1.3	.35 ± .05	7.3 ± 1.1
	♀	12	4.76 ± .10	1.1	.35 ± .07	7.3 ± 1.5
F_1	♀ Dec. 1912a	11	1.36 ± .09	.9	.31 ± .07	22.7 ± 5.1
	♂ Dec. 1913v	25	1.24 ± .03	.5	.14 ± .02	11.4 ± 1.6
	♂ Aug. 1913o	29	2.56 ± .05	1.0	.25 ± .03	9.8 ± 1.3
	♀	29	2.30 ± .06	1.2	.35 ± .05	15.0 ± 2.0
	♂ Aug. 1914c	42	2.31 ± .04	1.2	.24 ± .03	10.6 ± 1.2
	♀	9	2.90 ± .13	1.0	.39 ± .09	13.6 ± 3.3
	♂ Aug. 1914a	25	2.22 ± .07	1.3	.36 ± .05	16.3 ± 2.4
	♀	30	2.74 ± .08	1.9	.45 ± .06	16.4 ± 2.2
	♂ Sept. 1914d	20	1.72 ± .10	1.5	.43 ± .07	25.1 ± 4.2
	♀	10	1.59 ± .14	1.4	.43 ± .10	27.2 ± 6.5
F_2	♂ Oct. 1914e	6	2.00 ± .32	2.4	.78 ± .23	39.1 ± 12.9
	♀	5	1.30 ± .31	1.9	.70 ± .22	53.8 ± 21.4
	♂ Oct. 1914g	17	2.15 ± .28	3.3	1.15 ± .20	53.4 ± 11.5
	♀	11	1.41 ± .17	1.7	.57 ± .12	40.4 ± 9.9
	♂ Nov. 1914q	13	.95 ± .12	1.5	.43 ± .08	45.8 ± 10.7
	♀	3	1.40 ± .06	.2	.10 ± .04	7.1 ± 2.9
Backcross to *philodice*	♂ Nov. 1914h	20	1.07 ± .16	1.9	.69 ± .11	65.2 ± 14.0
	♀	35	1.19 ± .08	1.7	.45 ± .05	37.7 ± 5.1
Backcross to *eurytheme*	♂ Nov. 1913s	63	1.77 ± .07	2.6	.55 ± .05	31.0 ± 2.8
	♀	29	1.82 ± .08	1.6	.44 ± .06	24.1 ± 3.3
	♂ Nov. 1913t	29	2.22 ± .13	2.7	.71 ± .09	32.0 ± 4.6
	♀ White only					
	♂ Dec. 1913u	36	1.99 ± .11	2.8	.68 ± .08	34.3 ± 4.5
	♀	14	2.05 ± .24	2.6	.88 ± .17	43.0 ± 9.5
1924 Kansas *eurytheme*	♂ Aug. 1924c	56	3.17 ± .12	2.9	.90 ± .09	28.5 ± 2.8
	♀	42	3.93 ± .17	4.1	1.13 ± .12	28.7 ± 3.2

SEASONAL VARIATION IN PIGMENTATION AND SIZE

As an example of seasonal difference between two broods with corresponding, or at least comparable, genetic constitution, we may compare the 25 F_1 ♂♂ in brood 1913v, emerged in December, with 30 F_1 ♂♂ of 1913o, emerged August 24 – September 19. Orange pigmentation of the former, winter brood (pupation began November 16) was reduced by seasonal conditions to an average of 1.24 ± .03 Levibond red units (fig. 2). In no individual did it exceed 1.5 (faint flush of red), varying downward within its narrow range to 1.0, at which by ordinary inspection no red was visible.

On the other hand, in the August–September F_1 brood, 1913o (pupation began August 15,

eclosion August 24 – September 19), the ♂ average in red was numerically twice as high, 2.56 ± .05, and similar to the averages of the F_1 broods of August, 1914, a = 2.2, c = 2.3. The lower limit in 1913o, 2.1, was far above that of 1913v, 1.0; the upper limit reaching 3.1 (*cf.* 1.5).

Measurements of the melanic pigmentation of the August–September vs. the December broods (under side of hind wings), also made with the Tintometer (blue units united with others of yellow and red in a combination visibly like the specimen), gave even more striking differences though in contrary direction to those for red. In an August F_1, 1913o, the average in blue (used to measure black) for ♂♂ was only 0.32, for ♀♀ 0.51; in a December F_1, 1913v, however, it was 2.06 for ♂♂, 2.52 for ♀♀.

It may be significant that this August–September F_1 brood, 1913o, like the corresponding 1914 broods a and c, was raised indoors in a greenhouse and exposed to higher temperatures than the fall-winter F_1 brood, 1913v, which was raised up to the time of pupation (November 16) out of doors.

Another F_1 brood, 1914d (fig. 2), which emerged September 1–13, only a week or two later in the season than 1913o and other August broods, resembled in orange pigmentation and melanism more closely the fall-winter brood 1913v than 1913o and the August broods of 1914. Like 1913v, it was raised outdoors and exposed to some very low temperatures; *e. g.*, the official minimum outdoor temperature at Hanover for August 24–25, 1914, was 42.9° F., and that of the night of August 25–26 was 39.0° F. On the following day, August 26, the pupae were brought into an evenly cool room (65° F.), and they began to emerge on September 1.

The brood's male average for red was 1.7 ± 0.10, intermediate between the averages of the December and August broods in question. Its range, like that of the brood 1913v, extended downward to 1.0, faintest flush of orange, but, unlike the December brood, it rose to 2.5, thus touching the average of the August brood.

The strong resemblance between the intermediate coloration of this September brood and that of the other emerging in December might be ascribed to the fact that both were raised outdoors and exposed to lower temperatures than the August broods raised in the greenhouse. How otherwise can we account for the fact that the intermediate, September brood 1914d (caterpillars in August, the first of them pupating during remarkably cold days) should contain individuals in which orange was reduced to the minimum (1.0) in red?

Until recently I have assumed that low temperature is the chief and perhaps the only factor reducing the intensity of orange and increasing that of melanic pigmentation in butterflies raised in late fall and winter. Even casual comparison of any two broods of somewhat similar genetic constitution raised in the greenhouse, one in summer, one in late fall, shows that the summer individuals are larger, more intensely orange (in *eurytheme* and its hybrids) and, on the under side of the wings, less intensely melanic; the winter specimens are smaller, paler in orange, and darker in melanic pigmentation of the scales of the under side.

Records of temperature in our greenhouse in 1914 indicate, however, that these seasonal differences observed in my cultures, just as in wild "*ariadne*," "*keewaydin*," and "*amphidusa*," are determined not only by low vs. high temperature but also by other seasonal conditions, such as nature of the food.

These records show that the average greenhouse daytime temperatures in November and December were actually higher (77.6° F. and 75.6° F.) than in September and October (74.0° F. and 74.2° F.), and yet the diminution of orange and increase of melanic pigmentation in the November–December butterflies raised in the greenhouse was extreme.

Greenhouse temperatures under which the larvae and pupae were raised in 1914, taken at various times between 9 a. m. and 5 p. m.

	No. of observations	Average temp. in shade
July } Aug. }	38	84.0° F. (85.5° F., if 4 direct sunlight readings are included)
Sept.	12	74.0° F. (77.0° F., if 1 direct sunlight reading is included)
Oct.	23	74.6° F. (80.5° F., if 7 direct sunlight observations are included)
Nov.	18	77.6° F. (82.0° F., if 3 direct sunlight observations are included)
Dec.	6	75.6° F. (74.4° F., if 1 record of 82.0° in partial sunshine is excluded)

The temporary rise of temperature in November was due to the first use of direct (thermostat-controlled) steam heat. A steam-pit in the adjoining basement was a constant source of indirect heating day and night and every month. The caterpillars feeding on potted white-clover

plants were more or less exposed to direct sunlight, but temperatures in the shade are more reliable. No records at night were made, but it is practically certain that when direct steam heat with thermostat control was used (November–December), night temperatures did not fall lower than the early morning records of August–October, such as:

August	16	6:00 a. m.	62° F.
August	21	9:15 "	66° "
September	8	9:00 "	62° "
September	12	8:30 "	53° "
October	28	7:00 "	67° "

Perfectly conclusive data bearing on the problem of temperature vs. other climatic conditions such as light are not available. No experiments planned for such tests were made.

However, a winter, greenhouse-bred F_1 species-hybrid brood, 1912a (pupated November 12–15, emerged November 29 – December 5; fig. 2), is also of interest when compared with the summer F_1 broods before mentioned. This consisted of 10 ♀ ♀ and 1 ♂. Its ♀ average in red, 1.36 ± .09, and range in red, 1.0–1.9, are similar to those of the December brood, 1913v, raised outdoors, in which:

25 ♂ ♂ gave an average of 1.24 ± .03; range in red between 1.0 and 1.5

5 ♀ ♀ gave an average of 1.14; range in red between 1.0 and 1.2

These F_1 winter averages for red are about half those of the F_1 summer broods, 1913o and 1914a and c, and were produced under approximately similar greenhouse conditions as regards temperature. Accordingly, the marked seasonal difference in orange coloration is due not so much to temperature as to other winter conditions.

The size of the butterfly is reduced, even more than the orange pigmentation, under moderately warm greenhouse winter conditions. The average wing expanse of these 10 ♀ ♀ of 1912a, for example, was 39 mm. (♀ *eurytheme* parent = 44.8 mm., ♂ *philodice* parent = 44.2 mm.). These measurements may be compared and contrasted with those of the summer indoor brood, 1913o: ♀ ♀ 47.8 mm., ♂ ♂ 47.5 mm. The ♀ *eurytheme* parent of this brood measured 53 mm., the ♂ *philodice* parent 45 mm.

It is not likely that the F_1 broods used in these comparisons are of precisely the same genotype in every detail; the *eurytheme* parents differed somewhat in strength of orange coloration. F_1 broods, as has been shown, are not highly variable, but it is possible that minor modifying genes may act upon the red, to intensify or reduce it. Such differences among F_1 individuals, however, are insignificant compared with the major genetic and environmental differences.

In general, F_1 broods are comparable, *inter se*, in measuring environmental influence. The variation in intermediate orange within any one of these broods is slight as compared with the wide range in *eurytheme* or in the F_2. As we have seen, the F_1 orange in summer is twice as brilliant as in December, and under warm greenhouse conditions in November–December the reduction in F_1 redness and in size still obtains.

Another example showing similar results was 1914i (fig. 1), a cross of two of the more pronounced orange individuals from a backcross with *philodice* (h^7 ♀ × h^3 ♂). These two heterozygotes for orange were mated October 22; eggs hatched November 1, pupation began November 20, and eclosion took place November 29 – December 15. This cross, equivalent to an F_2 as regards orange, would be expected under *autumnal* conditions to produce some individuals similar in *eurytheme*-like brightness in red to the October F_2, 1914g, some ♂ ♂ of which (fig. 2) measured 3.8–4.1, or to the October F_2, 1914e, measuring 3.0. As a matter of fact, the two brightest ♂ ♂ of this winter brood, 1914i (eclosion December 8–10, measured only 2.2 and 1.8, and the brightest ♀ only 1.9; the heterozygous parents were: ♂ 1.9, ♀ 1.6 (slightly worn). Wing expanse in 1914i averaged 38.97 mm. in ♂ ♂, 39.33 mm. in ♀ ♀, *i.e.* similar to that in the other winter broods 1912a and 1913v, but several millimeters less than in the autumnal and summer ancestors. It is noteworthy that the average greenhouse temperature recorded for November, 1914, when these 1914i were caterpillars (pupation began November 20), was 77.6° F., higher than in September and October. The small size and reduced orange coloration, in spite of the high temperature, were striking.

Again, the backcross to *philodice*, 1914h (fig. 2), from which came the parents of 1914i, varied downward through the range of *philodice* to 0.1 (in ♂ ♂), upward to 2.0 (♂ ♂ and ♀ ♀). Pupation began October 5, eclosion October 15. The caterpillars therefore were exposed to diurnal temperatures averaging 74.6° F. and to autumnal illumination intermediate between winter and summer intensities. In accordance with these and other autumn conditions, the maximum in

red, 2.0, in this October backcross is considerably below F_1 summer averages, viz, 2.2 ± .07 for ♂♂, 2.7 ± .08 for ♀♀ in 1914a, the F_1 brood from which 1914h came. Environments being equal, one would expect this backcross to cover the F_1 range; actually it covered only the lower part of the range.

Finally, in backcrosses of *eurytheme* ♀♀ to F_1 ♂♂ (eclosions November–December, 1913, and December, 1913 – January, 1914), orange intensity in each sex reached a maximum of only 3.7 (fig. 2). Such a backcross would be expected to cover the upper limits of *eurytheme*'s range, but this maximum reached only the summer *averages* in ♀♀ of wild *eurytheme* (viz, 3.8 ± .25 in ♀♀ of 1913m; 3.5 ± .14 in ♀♀ of 1913b), the maxima of which were 4.6 and 4.7, the upper limits of the ♂♂ being still higher, viz, 5.0 and 5.3.

It is evident from these winter backcrosses that intensity in red is scaled down to levels far below genetic expectation for summer conditions and in spite of the fact that high greenhouse temperatures were maintained.

Low temperatures obviously check feeding and limit metabolism and growth, and so might diminished illumination and short days. Thus low temperature *per se* may not be, as I had supposed, the chief cause (directly affecting the pigments) of the decrease in orange and increase in black observed in these winter broods.

Specimens of *C. eurytheme* sent to me by Mr. E. H. Floyd, of New Orleans, collected early in January at Baton Rouge, La., and hence having passed the last part of their larval and all of their pupal stage during December, show greatly reduced size and paleness of orange pigmentation even more extreme than in pure *eurytheme* raised in a greenhouse at Hanover, N. H.

The average temperature for December at New Orleans for 48 years has been 55.3° F. Baton Rouge is about 100 miles north of New Orleans, and the temperature is nearly the same in both places. The maximum temperature at New Orleans in December, 1938, was 79° F., and mean maximum 64°, whereas the recorded temperatures in the shade in my greenhouse ran from 79° to 70°. The minimum at New Orleans for December, 1938, was 33° F., and the average minimum 47°. Records of minima in the northern greenhouse are lacking, but probably they were well above the outdoor records in Louisiana, since the greenhouse was under thermostat control set at 65°. The strikingly similar results (small size and diminished redness) are evidently determined partly but not wholly by low temperature.

As to illumination, we find no marked shortness of day in Louisiana. At Baton Rouge (*U. S. Nautical Almanac*) the length of the shortest day, December 22, is 10.13 hours, vs. 13.87 hours of night. (Sun rises at 6:52 a. m.; sets at 5:04 p. m.) Shortness of day, so marked at the northern latitude and in a partly shaded greenhouse, can hardly apply to conditions in Louisiana.

There remains one other ecological factor bearing on growth-restriction and diminished orange pigmentation, viz, condition of the food-plant. At Hanover, N. H., severe frosts begin about October 10. Clover leaves exposed to the first frosts are partly frozen; plants brought into the greenhouse in October are neither thrifty nor succulent. The same is true of Louisiana clover out of doors in December. I am forced to conclude that less nutritious food and diminished feeding by the larva are largely responsible for the small size and lower grade of orange pigmentation in the winter butterfly.

As is well known, melanic pigmentation is the result of the oxidation of tyrosin promoted by tyrosinase, a reaction which I had regarded as favored by cold and wet conditions because melanic pigmentation is often associated with such conditions. May it not be due primarily to a diminished rate of metabolism and only secondarily to low temperature and high humidity?

Conclusions as to seasonal variation in Colias.— These observations show that under practically constant average temperatures in the greenhouse the pronounced seasonal variations in orange pigmentation, melanism, and size of the butterfly, that are observed in the field farther south, nevertheless occur. One is forced to the conclusion that condition of the food-plant, more than low temperature and diminished illumination which control the activity of the caterpillars, is the chief factor differentiating "*ariadne*" from "*keewaydin*" and "*amphidusa.*" Nutrition and rate of metabolism are fundamental in the determination of seasonal variations in insects.

Invasion of *eurytheme* Eastward

In recent years *eurytheme* has spread eastward from the Mississippi Valley into the territory of *philodice* and has become established with its (*eurytheme-philodice*) hybrids at various places along the Atlantic seaboard.

In 1889, Scudder (p. 1131) wrote: "East of the Mississippi Valley it occurs sparingly and disappears entirely at the Alleghenies with the few exceptions which we shall shortly note." "To the east, west of the Alleghenies, it seems to have followed down the St. Lawrence valley." Single specimens were noted from Montreal and Quebec, Montpelier, Vt., Belmont and Wollaston, Mass., Norwich, Conn., Mount Desert, Me., Newcastle, Del., and "once" in Maryland.

Clark (1932), on the authority of C. S. Brimley, states that *eurytheme* has been common in North Carolina since 1900, though it did not occur in West Virginia in 1889, when W. H. Edwards (1884, 2nd series of 1868–1897) was living at Coalburg, just west of the Alleghenies, near Charleston. He concludes: "Before 1889 *C. eurytheme* did not occur in the mountains or on the Atlantic watershed. But during the next 10 years it filtered through the mountain valleys and became common in North Carolina and Southern Virginia."

At Washington, D. C., the first well authenticated occurrence mentioned by Clark (1932) is of a single male taken in 1904; another was taken "about 1910," and a female in 1923. (In September, 1923, several males and one female were caught at Philadelphia and described by Napier (1924) as the first recorded occurrence there.) In 1925 and especially in 1926 it was found near Washington in increasing numbers, becoming in 1927 nearly or quite as abundant as *philodice*. In 1928 and 1929 it was slightly less common, but in 1930 it outnumbered *philodice*.

In 1927, at Brooklyn, N. Y., F. E. Watson (1929) captured several specimens of *eurytheme* (*amphidusa* and its white female) and others again at Long Beach, L. I., N. Y. In 1928 it "suddenly appeared in considerable numbers everywhere around Ithaca," N. Y. "The species has not been previously recorded from Ithaca." (Klots, 1929.) Brower (1929), following up the occurrence of *eurytheme* at Ithaca in 1929, from July 6 onward, says: "It appears to be slightly more abundant than last year."

The wave of infiltration of 1923–25, noted at Philadelphia and Washington, reached Massachusetts in 1925, when Clark (1925) captured three fresh males at Ipswich in August and saw another at Essex. In 1930 he again observed it near Boston. Richard T. Holway, in an unpublished master's thesis, writes: "At Amherst, Mass., in the fall of 1932 it occurred in the ratio to *philodice* approximately 1 to 10." Several specimens were taken with varying amounts of the typical *eurytheme* orange on the wings.

Incursion into New Hampshire and a 1940 Census

In 1913 and 1914, when most of the breeding experiments already described were made, *eurytheme* did not occur at Hanover, N. H., nor was it seen during the next 20 years; in 1934, however, a small incursion took place. From a typical orange female caught August 31, already fertilized, two generations of pure *eurytheme* were raised; two males also were seen on that date, and on September 5 another female was caught. In 1935 only two or three individuals were observed; none in 1936 or in 1937. In 1938, three orange individuals were seen, the first two (September 5 and 25) at the same spot. Their pale orange color indicated possible hybridization. On October 3 the third was seen. Meanwhile the fall brood of *philodice* was present in great abundance.

Even *philodice*, usually abundant at Hanover, N. H., was exceedingly rare in 1939. None of the first generation was seen during May, only one in June, and none in July until the 28th—a small ♀; early in August two male representatives of the second generation were observed, but not until the last fortnight of September and the first half of October did *philodice* become fairly common. It is not surprising, therefore, that *eurytheme* and its hybrids were correspondingly rare. An orange individual was seen on June 18 but no *philodice*, though a single one had been noticed a week previous to that; on August 12 an orange individual and one *philodice* were observed. When the fall brood of *philodice* had become fairly common and the first hard frost had occurred on October 16 (which regularly results in the death of the fall brood of imagines by destroying the flowers that are their food supply), a third orange individual was seen.

In 1940 the spring and summer generations of *philodice* were small, but by September 5, when the third or fall brood was beginning, *philodice* became exceedingly abundant, continuing so until the first killing frost, on October 16. The first *eurytheme* observed (a typical ♀) was seen on August 27 and another (worn ♀) on September 10. By this time it was decided to make a statistical examination of the abundant *Colias* population, the result of which was that, within a radius of about 1 mile, 648 *philodice*, 5 *eurytheme* (4 ♂♂, 1 ♀), and 5 hybrids (♂♂) were

	PHILODICE			EURYTHEME	HYBRIDS	
	♂	♀ YELLOW	♀ WHITE			
SEPT. 11	22	9		1♀		MINK BROOK (BARBARA BROWN)
14	15	4	3	1♂		NEAR PUTNAM'S (B. BROWN)
14	6	2		1♂	1♂ F_1	MEETINGHOUSE HILL (ANN VERRIEST)
15	9	5	3		1♂ BACKCROSS	CHASE FIELD (B. BROWN)
28	29	4	5			CHASE FIELD (B. BROWN)
28	28	19	1		1♂ BACKCROSS	OCCOM RIDGE
30	9	8	1	1♂		OCCOM RIDGE
OCT. 1	42	21	3			NEAR CHIVERS'
1	61	11				SKI JUMP (DR. R. WEAVER)
2	14	14	1	1♂		OCCOM RIDGE
3	11	5	2			OCCOM RIDGE
4	9	8	2			OCCOM RIDGE
5	33	24	8			OCCOM RIDGE
					1♂ F_1, 1♂ BACKCROSS	OCCOM RIDGE
7	10	14				OCCOM RIDGE
7	37	13				LEWISTON
9	4	5	2			OCCOM RIDGE
10	11	6	1			OCCOM RIDGE
11	11	5	1			OCCOM RIDGE
11	10	8	2			CHOATE ROAD (W. J. SCHALDACH)
12	16	8	4			OCCOM RIDGE
14	13	8	3			OCCOM RIDGE
16	4	1				OCCOM RIDGE
	404	202	42	4♂♂, 1♀	2 F_1♂♂, 3♂ BACKCROSS	

FIG. 4. *Colias philodice* (yellow), *C. eurytheme* (orange), and their species hybrids (pale orange), caught (and preserved) by various observers within a radius of about a mile at Hanover, N. H., September 11 to October 16, 1940.

Total sample of *C. philodice* population 648
Total sample of *C. eurytheme* population 5
Total sample of species-hybrids population 5
Total sample of foreign population (*C. eurytheme* and hybrids) ..... 1.5 percent

caught and preserved (figs. 4 and 5). Thus 1.5 percent of this sample of *Colias* population consisted of *eurytheme* and hybrids.[2] The 5 hybrids were identified as almost equally F_1 and paler, possibly backcross individuals, viz, 2 F_1 ♂♂ and 3 ♂♂, either F_1 or backcross to *philodice*.

GEOGRAPHICAL DISTRIBUTION OF *Colias eurytheme*; THE *eriphyle-philodice* COMPLEX AND NATURAL HYBRIDS

Colias eurytheme presumably came from (or went to) Asia, spread southward along the Pacific coast, thence eastward over the Mississippi Valley to the Alleghenies and, recently, to certain regions along the Atlantic coast.

It is generally regarded as the North American representative of *C. chrysotheme* Esp. of southeastern Europe, Asia Minor, and southeastern Siberia. Its larva and pupa, as figured in color by May (1894), support that assumption even more than does the small, heavily marked butterfly of eastern Europe. Its Siberian form, *siberica* Gr.-Grsh., more closely resembles our *eurytheme*. A vetch, *Vicia hirsuta* Koch, is said to be its food-plant. I have seen *C. eurytheme* laying at Hanover on *Vicia crassa* L. as well as on alfalfa and on white and red clovers. At a high altitude (10,000 feet) above Centennial, Wyoming, Dr. Klots found it (a large "*amphidusa*") laying on *Astragalus alpinus* L.

[2] Those regarded as F_1 ♂♂ measured 1.9 and 2.2 Levibond units of red; the 3 F_1 or backcross ♂♂, 1.3, 1.4, and 1.6. The *eurytheme* ♂♂ measured 3.3, 3.5, and 4.8 in red; the *eurytheme* ♀, 3.8 in red.

From this wide-ranging orange species has arisen a species-complex consisting of two yellow forms, *eriphyle* and *philodice*, more closely allied to each other than to *eurytheme*, with which each more or less frequently hybridizes with a varying degree of fertility.

Numerous experiments have shown me that these western and eastern yellow forms breed true and maintain their identity when occupying, as one of them often does, the same region as the generally larger and more vigorous parent species. It should be noted that the male in neither *eriphyle* nor *philodice* is ever orange, though the female *eriphyle* often, and in fact generally beneath the front wings, retains traces of it.

C. philodice long ago spread over the Mississippi Valley and reached the Atlantic seaboard. *Eriphyle* has continued to occupy the Great Basin and Columbia River plateaus (between the Sierra Nevada - Cascade Ranges and the Rocky Mountains), the mountain meadows among the Rocky Mountains, Montana, and North Dakota, and it also ranges northward into Alberta and British Columbia.

It is a curious fact that *eriphyle* has not established itself west of the Sierra Nevada; though

	PHILODICE			EURYTHEME	HYBRIDS
	♂	♀ YELLOW	♀ WHITE		
SEPT. 28	28	19	1		1 ♂ BACKCROSS
30	9	8	1	1 ♂	
OCT. 2	14	14	1	1 ♂	
3	11	5	2		
4	9	8	2		
5	33	24	8		1 ♂ F_1 + 1 ♂ BACKCROSS
7	10	14			
9	4	5	2		
10	11	6	1		
11	11	5	1		
12	16	8	4		
14	13	8	3		
16	4	1			
	173	135	26	2 ♂♂	3 ♂♂, (1 F_1 + 2 BACKCROSS)

FIG. 5. *Colias philodice* (yellow), *C. eurytheme* (orange), and their species hybrids (pale orange), caught (and preserved) in one garden at Hanover, N. H., September 28 to October 16, 1940.

Total sample of *C. philodice* population 334
Total sample of *C. eurytheme* population 2
Total sample of species-hybrids population 3
Total sample of foreign population (*C. eurytheme* and hybrids) ..... 1.47+ percent

single migrants, or mutants, have been found rarely in that region (William Hovanitz, *in litt.*; also Gunder, 1924). At one point north of Mount Shasta of the Cascades, *eriphyle*, extending westward, has reached Yreka, a few miles southwest of the point where the Klamath River crosses the California-Oregon border through a gap in the Cascade Range. "This is typical high desert of the Great Basin type" (Hovanitz).

There is a possibility, however, suggested to me by Dr. Klots, that the small yellow *C. harfordi* of the San Bernardino Mountains, the foodplant of which is *Astragalus crotalariae*, may be a southern derivative of *C. eriphyle*.

C. eriphyle, first described by W. H. Edwards (1876) from specimens taken in south central British Columbia, is mentioned by Wright (1906), who says: "Eriphyle is not known on the West Coast to the south of the Canada line and the species extends eastward through Montana, and south to Colorado." He adds that it is likely to be "found plentifully in some parts of East Washington, East Oregon and Idaho." Specimens from Montana, eastern Washington, and Pueblo, Colorado, are figured in one of his colored plates.

On the plains of Kansas and Nebraska occurs a yellow race intermediate between *eriphyle* and *philodice*, which for several years I labelled "*eriphyle*," but after thorough study of broods of that form from Colorado (Tolland), Wyoming, and Alberta, and of my notes on their breeding habits, I have come to regard it on the whole as more nearly identical with the eastern *philodice* than with *eriphyle* of the western mountains.

Notwithstanding the minor differences in color between the Kansas and the eastern *philodice* noted by Field (1938), I have found between them perfect mating affinity and, so far as tested, no lack of fertility.

This conclusion relieves somewhat the necessity of seeking an unknown and necessarily arbitrary boundary between *eriphyle* and *philodice*, such for instance as the Mississippi River, since the habitat of *eriphyle*, in accordance with its original description, would be limited to the northwestern mountains and plateaus already mentioned.

It is worth noting, however, that there are no barriers except altitude and distance between the Kansas-Nebraska plains and the Colorado-Wyoming mountains, for the valleys of the branches of the Platte River lead directly from one to the other (map 1).

Colias eriphyle Is Not *C. eurytheme*; Historical Review

C. eriphyle frequently has been confused with *eurytheme*. Thus J. A. Comstock (1927) describes *eriphyle* as a "high altitude summer form (of *eurytheme*) often found flying in association with *amphidusa*" in the Mono Basin and high plateaus of northern California. Its smaller spring form, *autumnalis* Ckll., is said to come from "overwintering chrysalids," which, by the way, is doubtful, for these *Colias* allies generally winter as half-grown larvae. "*C. autumnalis*" is certainly the spring form of *eriphyle*, but the summer form of *eurytheme* is, of course, the large, brilliant orange "*amphidusa*" and not the smaller, yellow *eriphyle*.

Scudder, in his excellent little book on the commoner butterflies (1899: 19), mistakenly mentions *eriphyle* as the *earliest* and the *latest seasonal* form of *eurytheme* "in the northern part of the range" of the species, the orange forms of which being interpolated between them. Thus he regards *eriphyle* as a local substitute for *ariadne*, the palest orange seasonal phenotype of *eurytheme*.

This rather wide-spread confusion is probably due, partially at least, to the classical breeding experiments of W. H. Edwards (1887*a*; 1897) and his conclusion that *eriphyle* is not a species, as he at first assumed, but merely a "form" of *eurytheme* such as "*keewaydin*" and "*amphidusa*."

These experiments were upon a yellow butterfly first described by him (1884) as *Colias hagenii*, the eggs, larvae, and chrysalids of which had been sent to him from Pueblo, Colorado. He described (1887*a*) the results of raising to the imago, between 1884 and 1887, ten lots of eggs from Pueblo, nine of which were said to be from *C. hagenii*. Closely following this, he wrote (1887*b*): "In my last paper I showed that *C. Hagenii* was a yellow form of *C. Eurytheme* Bois., and I am now prepared to say that *Hagenii* is identical with *Eriphyle*, and the name gives way to this." In conclusion: "The name *Hagenii* therefore is sunk, and this form will be known in the future as Colias EURYTHEME, tetramorphic form ERIPHYLE (pronounced E-riph′-y-le)."

Thus he reduced *eriphyle* to the same level as the three seasonal variations of *eurytheme* (*ariadne*, *keewaydin*, *amphidusa*), which are now known to be genetically identical "forms" of *eurytheme*.

In 1897 (series 3, *Colias* III) Edwards summarized again these observations first recorded in 1887, replacing the name "*Hagenii*" by "*eriphyle*," which he treated as a form of *eurytheme* rather than as a minor but independent species.

It is important to examine critically the observations on the ten lots of eggs which led to this conclusion. They represent only a part of the many consignments of eggs laid at Pueblo, Colorado, and sent to him by Mr. H. W. Nash with the (dead) females which laid them. They were reared at Coalburg, West Virginia, on white clover, no doubt with meticulous care.[3]

Nine of the mothers were said to be *eriphyle;* the offspring of six of them were likewise all *eriphyle.* All eggs received after 1884 (1885, 1886, and 1887) produced only *eriphyle* except that one of the 1887 lots included a single *eurytheme* female with three of *eriphyle*, the 17 males all being *eriphyle.* If this anomalous *eurytheme* female was included by accident (as is certainly the case), then the number of lots breeding true to *eriphyle* would be not six but seven in nine.

Of the five lots received in 1884, two produced only *eriphyle*, but three (on which *eriphyle*'s status as a "form" of *eurytheme* apparently has rested) were peculiar and require closer examination.

One of the three (lot 2, June 7, 1884), though said to be from one of the nine *eriphyle* mothers, produced only *eurytheme:* 11 ♂♂ and 4 ♀♀, of which 3 were white. In all probability the mother was not *eriphyle* but a white *eurytheme*, which normally would produce just such a brood as this. If *eriphyle*, she might have mated with a ♂ *eurytheme* carrying the gene for female whiteness, but if so, all the hybrid orange offspring would have been conspicuously (July 6–9) *pale* orange, which is far more than unlikely. Evidently only eight of the ten mothers were *eriphyle*, two were *eurytheme.*

Later in the same month *and on the same day* (June 27, 1884)[4] came two lots, nos. 3 and 5, certainly very badly mixed. Lot 3, from *eriphyle* ♀, produced 3 ♂♂ and 5 ♀♀ of *eriphyle*, with which were 4 *eurytheme* ♀♀. Lot 5, from a ♀ *eurytheme*, produced 2 ♂♂ and 1 ♀ *eurytheme* and 3 ♂♂ and 3 ♀♀ *eriphyle.* Eclosion being in midsummer when *eurytheme*'s colors are brilliant orange, hybridization, had it occurred, would have been easily detected by marked paleness in the *eurytheme* offspring. Since the two lots arrived by the same mail in hot weather as young larvae, a mix-up en route is not impossible, even if it had not already occurred at Pueblo.

Accordingly, we may be certain that the questionable lots 2, 3, and 5 in no way contradict the conclusion afforded by the others, viz, that *eriphyle* of Pueblo, Colorado, is of an independent, true-breeding minor species, as I have found to be the case at other western localities, and not a mere "form" of *eurytheme.*[5]

Retrograde Variations in Red in Females of Geographical Races of *eriphyle-philodice*

It will be advantageous to follow geographical lines in recording my studies of the various races of *eriphyle*, beginning with the Kansas and Nebraska forms intermediate between *philodice* and *eriphyle* (but which are in my opinion more properly called *philodice*), and then moving westward, taking up one by one these yellow races in Colorado, Wyoming, Alberta, Oregon, and finally eastern California, where William Hovanitz is now making an intensive survey.

I cannot claim to have made more than a superficial study of the geographical races. The samples of these populations which I have examined may not be typical of each, as to breeding behavior and coloration, but it is hoped that these records may be of use in more detailed studies, which should of course take account of the striking seasonal variations.

[3] Often the eggs and young larvae sent by mail failed to reach him alive; and disease destroyed many of the earlier cultures bred "in glasses," so that later he successfully used sods of white clover in pots. The eggs often hatched before they reached him, for he says: "When young larvae were received," they were "placed on the leaves and covered with a muslin bag."

[4] In 1897 the date of lot 3 (mixed brood) is printed as "June 7" (not "27" as in 1887), making it identical with that of lot 2 (*eurytheme* from white mother). I am following the earlier (1887) and probably correct version, but, if that of 1897 is accurate, the same criticism would apply equally well to the mixture in lot 3.

[5] Dr. Hovanitz writes me that he finds nothing incongruous in these cultures, assuming that any slightly orange (hybrid) individual would have been called by Edwards "*eurytheme.*" Edwards stated that he never had seen a "live *eurytheme*" (wild), and he could have known nothing of hybrids. Accordingly, no mix-up en route need be postulated. The (recessive) *eriphyle* mothers of lots 2 and 3, having mated with two hybrid orange males, the first of which carried the gene for female whiteness, would produce such mixed broods. Both parents of mixed lot 5 would have been orange hybrids, and no pure *eurytheme* offspring were in any of the lots. Hovanitz avoids "hybrid" by using "*chrysotheme*" to cover *eurytheme*, *eriphyle*, and their natural hybrids.

Measurements of traces of red in the females of yellow (*philodice-eriphyle*) stock show clearly the gradual increase in intensity as one passes westward and then northward from the plains of Kansas and Nebraska through the succession of Rocky Mountain localities, Colorado, Wyoming, and Alberta, from which I have had my stock (fig. 6).

If these yellow races were long ago derived from the orange species by a series of loss mutations beginning in western Canada and gradually reducing the intensity of traces of red, the result might be like this series of measurements considered inversely, leading finally in the east to the almost pure yellow *philodice* of New Hampshire and of other Eastern States prior to the recent invasion by *eurytheme*. Remaining in the far West along the California coast west of the Sierra Nevada, in Arizona, Colorado, and Kansas, is a relatively pure orange *eurytheme*.

Along with the yellow races of the northwestern mountains, the sturdier orange *eurytheme* long ago spread eastward to the Alleghenies and, within more recent times, into New England.

Both stocks maintain themselves equally well on white clover, *Trifolium repens*. Egg-laying on red clover (*T. pratense*) is more difficult because the hairs of the under surface of the leaf interfere with attaching the eggs. I have some information from observers in the West that various wild vetches and lupines attract *eriphyle*, while *eurytheme* pays less attention to these particular members of the Leguminosae and lays chiefly on alfalfa. Much more information along this line is needed. Perhaps the luxuriant, succulent alfalfa has had much to do with the well-known larger size and greater vigor of *eurytheme*, whereas *eriphyle* has been able easily to maintain itself in mountain pastures where *eurytheme* is not found and perhaps would not thrive. Thus, Dr. P. W. Whiting (August, 1922) in Wyoming found "nothing but yellows"[6] around Centennial (8,000 feet). "Females were laying on various vetches and lupines. All were yellow, looked just like *philodice*, occasional orange suffusion on under side of primaries." My Wyoming stock came from one of these females. "In Nebraska," he wrote, "the yellows all seemed rather small. The orange were all large. The whites [presumably *eurytheme* females] were all large." "At Iowa City orange *Colias* does not occur. Yellows are fairly frequent."

[6] Successive generations of *eriphyle* are not precisely simultaneous with those of *eurytheme*.

Males of diverse yellow species and races of *Colias* are so slightly variable in the red component of their color that they are of much less interest in the present study than females. They will be considered briefly after the following account of the *philodice-eriphyle* females.

It is evident from figure 6 that traces of redness in the yellow females are generally stronger on the under side of the front wing than on the upper surface. Even in the New Hampshire *philodice*, in which redness is hardly visible at all by casual inspection, this difference between the two surfaces is detected by Levibond measurements (here multiplied by 10 to avoid decimal fractions). Thus in my 1940 September survey, 30 wild females measured, above, 6–8 units; below, 7–9. Expressing the upper surface as numerator, the lower as denominator, the result in red units × 10 was:

$$\frac{6}{7}\ \frac{6}{8}\ \frac{6}{9}\ \frac{7}{7}\ \frac{7}{8}\ \frac{7}{9}\ \frac{8}{8}\ \frac{8}{9}$$

$1 + 4 + 1 + 1 + 7 + 10 + 2 + 4 = 30$ individuals

Measurements of the upper surface of three New Hampshire broods of *philodice* (fig. 6) range from 0.2 to 0.9, with modes at 0.3, 0.6, and 0.9, the last being a close approach to clearly visible orange.

In the Kansas *philodice*[7] the mode stands at 0.8 for the upper side; in the Nebraska, at 0.9.

Both of these prairie broods differed widely from eastern *philodice* in the large measure of orange on the under side of the front wing, a prominent characteristic of *eriphyle*. Whatever we choose to call them, it is interesting to note that the under-side mode of both prairie broods and of the Colorado (fig. 6) is exactly the same (1.6), though in the Nebraska stock the majority (20 out of 32) are less red than this, the average being only 1.44. The Colorado *average*, 1.8, on the other hand, exceeds the mode, approaching the high under-side average for Wyoming, 2.08.

Returning to the upper-side red-tinge measurements of *eriphyle* females (fig. 6), we find that the mode for both Colorado and Wyoming is

[7] I have elsewhere discussed my reasons, based on crossmating behavior and interfertility with New Hampshire *philodice*, for calling these prairie broods *philodice*, but I would not quarrel with anyone prefering to name them *eriphyle* who can, at the same time, establish a sounder geographical boundary limit between *philodice* and *eriphyle* than that between the prairies and the mountains. The Kansas and Nebraska broods are, in fact, as far as these measurements are concerned, intermediate between *philodice* and *eriphyle*.

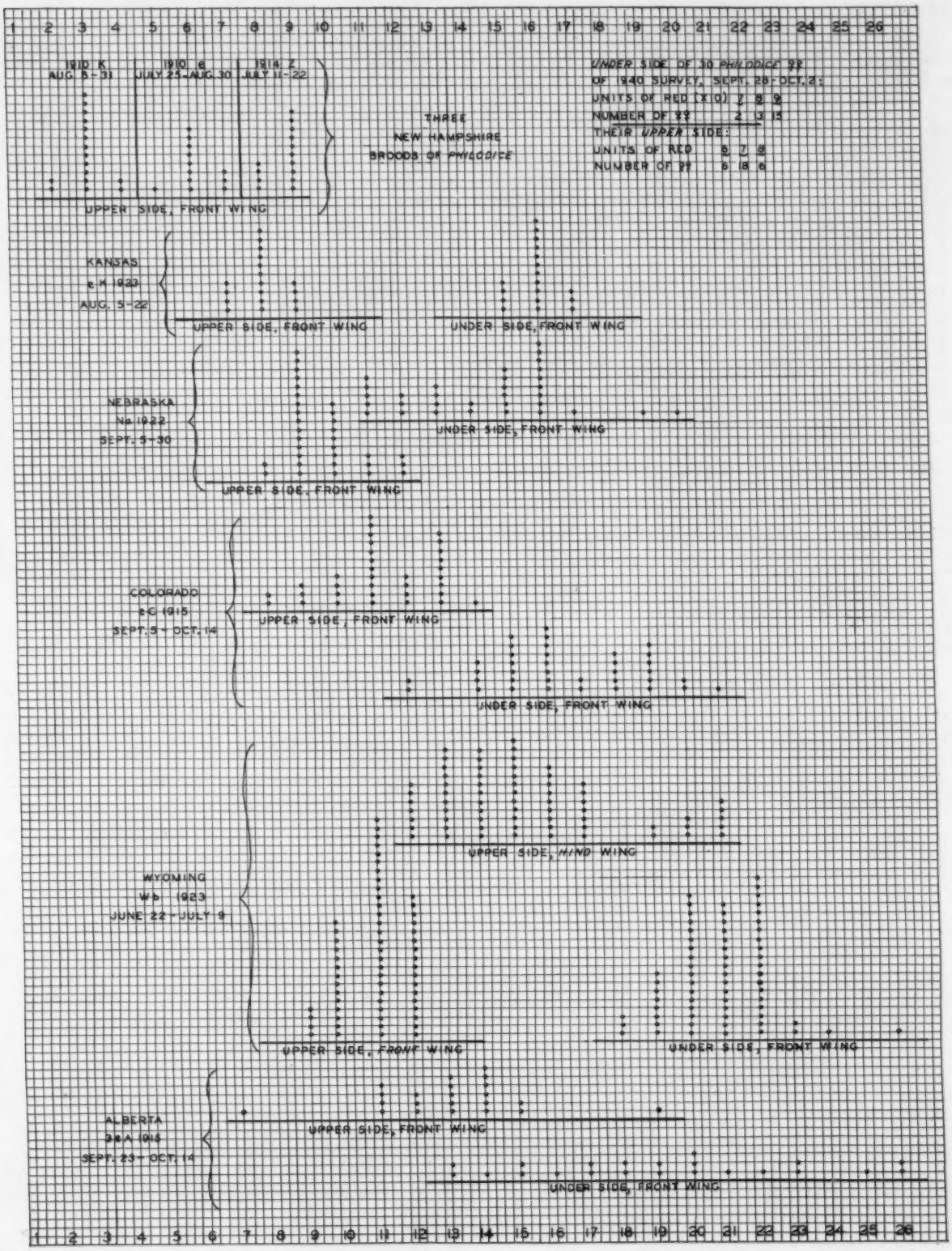
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26
1910 K
AUG. 5-31
1910 G
JULY 25-AUG. 30
1914 Z
JULY 11-22
UPPER SIDE, FRONT WING
THREE
NEW HAMPSHIRE
BROODS OF PHILODICE
UNDER SIDE OF 30 PHILODICE ♀♀
OF 1940 SURVEY, SEPT. 28-OCT. 2:
UNITS OF RED (X10) 7 8 9
NUMBER OF ♀♀ 2 13 15
THEIR UPPER SIDE:
UNITS OF RED 5 7 8
NUMBER OF ♀♀ 6 18 6
KANSAS
♂ K 1920
AUG. 5-22
UPPER SIDE, FRONT WING
UNDER SIDE, FRONT WING
NEBRASKA
Nb 1922
SEPT. 5-30
UNDER SIDE, FRONT WING
UPPER SIDE, FRONT WING
COLORADO
♂ C 1915
SEPT. 5-OCT. 14
UPPER SIDE, FRONT WING
UNDER SIDE, FRONT WING
UPPER SIDE, HIND WING
WYOMING
Wb 1923
JUNE 22-JULY 9
UPPER SIDE, FRONT WING
UNDER SIDE, FRONT WING
ALBERTA
♂ A 1913
SEPT. 23-OCT. 14
UPPER SIDE, FRONT WING
UNDER SIDE, FRONT WING
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26

FIG. 6. Measurements of red (Levibond units × 10) in (yellow) females of *philodice* and *eriphyle*. Redness gradually increasing into distinct visibility in *eriphyle* females.

SOURCE	SPECIES	MOTHER OR PARENTS	ECLOSION DATES	YEAR AND NAME OF BROOD	YELLOW MALES	YELLOW FEMALES	WHITE FEMALES	ORANGE MALES	ORANGE FEMALES	WHITE FEMALES
KANSAS (MANHATTAN)	*PHILODICE*	WILD WHITE ♀	AUG. 5–22	1923 eK	43	29	27			
	PHILODICE	cK[66] ♀ × *PHIL* (N.M.) ♂	SEPT. 30 – OCT. 15	1923 eKa	4	18				
	EURYTHEME	WILD WHITE ♀	AUG. 11 – SEPT. 6	1923 Ka				44	6	16
	EURYTHEME	Ka[37] ♀ × Ka[43] ♂	OCT. 12–30	1923 Kb				21	1	11
	EURYTHEME	WILD ORANGE ♀	JULY 14 – AUG. 6	1923 Ma				185	193	
	EURYTHEME	WILD ORANGE ♀	AUG. 16 – SEPT. 4	1924 c				62	61	
NEBRASKA (KEARNEY)	*PHILODICE*	WILD YELLOW ♀	SEPT. 5–31	1922 Na	90	68				
COLORADO (TOLLAND)	*ERIPHYLE*	WILD YELLOW ♀	SEPT. 5 – OCT. 15	1915 eC	13	50				
	EURYTHEME	WILD ORANGE ♀	SEPT. 1–20	1915 eu				16	14	
WYOMING (CENTENNIAL)	*ERIPHYLE*	WILD YELLOW ♀	OCT. 3–27 MAY 8 – 11	1922 1923 Wa	25	3				
	ERIPHYLE	Wa ♀ × Wa ♂	JUNE 23 – JULY 9	1923 Wb	85	95				
ALBERTA (MIDNAPORE NEAR CALGARY)	*ERIPHYLE*	WILD YELLOW ♀	SEPT. 16 – NOV. 12	1915 1eA	32	16				
	ERIPHYLE	WILD YELLOW ♀	SEPT. 23 – OCT. 14	1915 3eA	26	22				

FIG. 7. Western broods mentioned in this section.

exactly the same, 1.1, having moved up one point from Nebraska and two from Kansas.

It is important to note, however, that the Colorado brood was of autumn eclosion, that of Wyoming of early summer (June 22 – July 9) and probably forced ahead of similar stock at the high altitudes of Wyoming (the females having immature ovaries). Hence we may regard the Wyoming measurements as higher than they would have been in September–October when the Colorado and Alberta broods emerged.

In Alberta the upper-side mode moves on from 1.1 up to 1.4. Comparing this with the September *eurytheme* × *philodice* F_1, 1914d (fig. 2), we find it is slightly more orange than a half of the females of this fall brood and than most of those of the winter brood, 1913v. It is a clearly visible orange. A single female of the Alberta brood exceeds its sisters in redness by several points, measuring 1.9; another anomalous individual is plain yellow, 0.7.

In view of the fact that the Wyoming brood was of early summer, it is not surprising that its *under-side* measurements (fig. 6) are well above those of Colorado and Alberta (Wyoming varying between 1.8 and 2.5, with most of the individuals at 1.7–1.9, whereas those of Alberta are scattered toward clear yellow as far down as 1.3).

A detail in regard to the Wyoming early-summer brood deserves special mention. It is a suffusion of pale orange over the *upper* side of the *hind* wing and strongest near the edge. This varies in redness from 1.2 to 2.1. A somewhat similar suffusion was seen in a few of the white *eurytheme* females of Kansas (1923Ka) and suggests a minor modifying gene expressing itself similarly, as to position, in closely related species.

Males of the *philodice-eriphyle* complex (fig. 7), even in those summer broods with some pale orange females, are always clear yellow above, never distinctly orange-tinted. The very slight (below 0.10) red component on the upper surface of these yellow males stands lowest in intensity in *philodice* of the east, in most broods of which it was 0.2, 0.3, or 0.4. In the Kansas eK brood the mode was 0.4 (0.3 to 0.6), not essentially different from that of an eastern brood.

In *eriphyle* proper the mode was 0.7 in the Colorado and Wyoming broods and slightly higher—0.8 (0.7–0.9)—in the Alberta brood.

An exceptional eastern brood, 1914z, however, reached this high average, and Na of Nebraska slightly exceeded it—0.8–1.0—verging toward orange.

In general, it is fair to conclude that the male *philodice* of the East does not differ, in the red

component, from the yellows of the western plains (Kansas and Nebraska), while the male of *eriphyle* proper, in Colorado, Wyoming, and especially Alberta, shows a slightly higher average.

The measure of yellow, naturally very much higher numerically than of red, and representing particularly brightness of color, varied around 60 in broods of eastern *philodice*. This held also for Nebraska and Colorado but rose to an average of about 70 in Wyoming and Alberta.

Breeding Experiments with *philodice-eriphyle* Stocks and Their Hybridization with *eurytheme*

Kansas Stock

From the point of view of inheritance of orange-red, study of my 1923 Kansas stock (fig. 7) is complicated by the fact that the two different broods originally employed, one of Kansas *philodice*, one of *eurytheme*, were both from white mothers. The *philodice* eggs were laid from July on; the *eurytheme*, as it happened, a week later; both broods emerged in August. It may be recalled that the wild white female in both *philodice* and *eurytheme* usually has been found to be heterozygous for the dominant female-whiteness, producing, after mating with an ordinary yellow (or orange) male recessive for white-female wing-color, both white and yellow (or orange) daughters in equal numbers (Gerould, 1923). If, however, she has mated with a son of a white female, there are even chances that he was, though yellow (or orange, if *eurytheme*), a carrier of the dominant gene for female-whiteness for which he is a virtual heterozygote. Such a heterozygous pair should produce three times[8] as many white daughters as yellow (or orange). This was evidently the case in 1923Ka (fig. 6), for "Ka" included (besides 44 males) 22 females, of which 16 were white (dominant) and 6 orange (recessive). Again in 1923Kb, both parents were probably heterozygous for female-whiteness, the offspring being 11 white and 1 orange ♀♀ and 21 ♂♂.

Of the Kansas *philodice* brood, 1923eK, however, merely the white mother was heterozygous for female-whiteness (the wild father, homozygous recessive), for there were equal numbers of white and yellow daughters, viz, 27 white and 29 clear yellow ♀♀ and 43 ♂♂.

Are the white females of the Kansas *philodice* visibly distinguishable from *eurytheme* from the same locality bred under similar seasonal and other conditions? To a large extent the two are sufficiently unlike to be separable without a breeding test, but there are middle-of-the-road individuals subject to doubt, and a further possibility that the white *eurytheme* female in question may be a *eurytheme-philodice* hybrid capable of producing both yellow and bright orange offspring, as well as white daughters.

The following facts, drawn from a comparison between 11 white *philodice*, "eK," females and 13 *eurytheme*, "Ka," females, may assist in making a reasonable guess as to the correct classification of other Kansas white females. (1) Size: the wing-spread of the "eK" (*philodice*) females varies from 42 to 47 mm.; that of "Ka" (*eurytheme*) females from 47 to 55 mm. (2) The black marginal hind-wing band in "eK" varies in width from 2 mm. (unspotted) to about 5 mm. (faintly spotted); in "Ka," from 3 mm. to 6 mm., with a corresponding amount of spotting. (3) The central spot of the hind wings in "eK" measures approximately from 2.7 to 5.3 in red; in "Ka" there is less variation in the *bright* orange of 5.0 to 6.0 red units. Thus in (3), and especially in (2), there is overlapping at the middle of the range, making identification difficult.

Another striking difference between the two broods is a pale orange suffusion over the upper surface of the hind wings in 9 (65 percent) of the *eurytheme*, "Ka," females, but lacking in "eK." In 5 "Ka" white females the pale orange is strong; in 4, faint; in 4, lacking. In one "Ka" female the pale orange extends forward over the posterior two-thirds of the front wings and measures 2.2 in red units.

Mating experiments with Kansas stocks resulted as follows: on August 15 two pairs of Kansas *philodice* were coupled; on August 18, three pairs of Kansas *philodice* female × New Hampshire *philodice* male; on August 23, one more pair of this last combination, a fertile mating, the yellow mother (eK^{88}) producing in early October a brood (eKa) of 18 yellow females and only 4 males. It was not only a predominantly female brood but the females were precocious, for in the earlier eclosions (September 30 – October 15) there was only 1 male to 18 females. On November 7 another male was

[8] Very frequently, and in fact usually, the ratio thus obtained has been 2:1 rather than 3:1, a peculiarity explained (Gerould, 1923) as the effect of a lethal gene eliminating homozygous white females. No lethal gene is indicated in this instance.

found dead in the cage and also a few half-grown larvae which, pupating November 22–24, produced in December two more males.

Thus there was no lack of mating proclivity between the Kansas yellow females and New Hampshire males, and no infertility was recorded, though the predominantly female sex ratio was quite unusual in *philodice*. The females of this "eKa" brood retain the trace of orange under the front wings characteristic of *eriphyle* and also of the Kansas *philodice* (*eriphyle*-like) mother. The tendency of the males to mature slowly perhaps may be also an *eriphyle*-like tendency (*cf.* Colorado stock).

Incompatibility or sterility between Kansas *philodice* females and *eurytheme* males, on the other hand, was shown repeatedly; *e. g.*, on August 23, 24 Kansas *philodice* females were caged with 13 fresh *eurytheme* (Ka) males and 2 much-worn eastern *philodice* males. Two matings occurred, a Kansas *philodice* ♀ × New Hampshire *philodice* ♂, producing the "eKa" already described, and a sterile cross-mating, Kansas *philodice* female × *eurytheme* male. The female laid infertile eggs.

The reciprocal cross-mating was also made (August 18) between a white *eurytheme* female and Kansas *philodice* male. No eggs were obtained from this cross. Numerous other attempts to get cross-matings between these two species failed.

No sterility was detected meanwhile in matings within *eurytheme*, such as that which gave Kb, already mentioned, and three pairs within that brood which produced numerous progeny (unsuccessfully hibernated).

The high degree of fertility within Kansas *eurytheme* is still better illustrated by a slightly older all-orange Kansas brood, 1923Ma (fig. 7), consisting of 193 ♀ ♀ and 185 ♂ ♂, and in the numerous *inter se* matings within this brood made for the purpose of studying inheritance of dorsolateral stripes and other color features in caterpillars (results unpublished).

NO. OF BUTTERFLIES MEASURED	RED UNITS X10 MEAN	RANGE	STANDARD DEV.	COEF. OF VAR.
1924c ♀ 42	39.3 ± 1.7	41	11.3 ± 1.2	28.7 ± 3.2
♂ 56	31.7 ± 1.2	29	9.0 ± 0.9	28.5 ± 2.8
1923 Ma ♀ 42	48.3 ± 1.3	34	8.9 ± 1.0	18.4 ± 2.0
♂ 56	37.7 ± 0.9	26	6.7 ± 0.6	17.8 ± 1.7

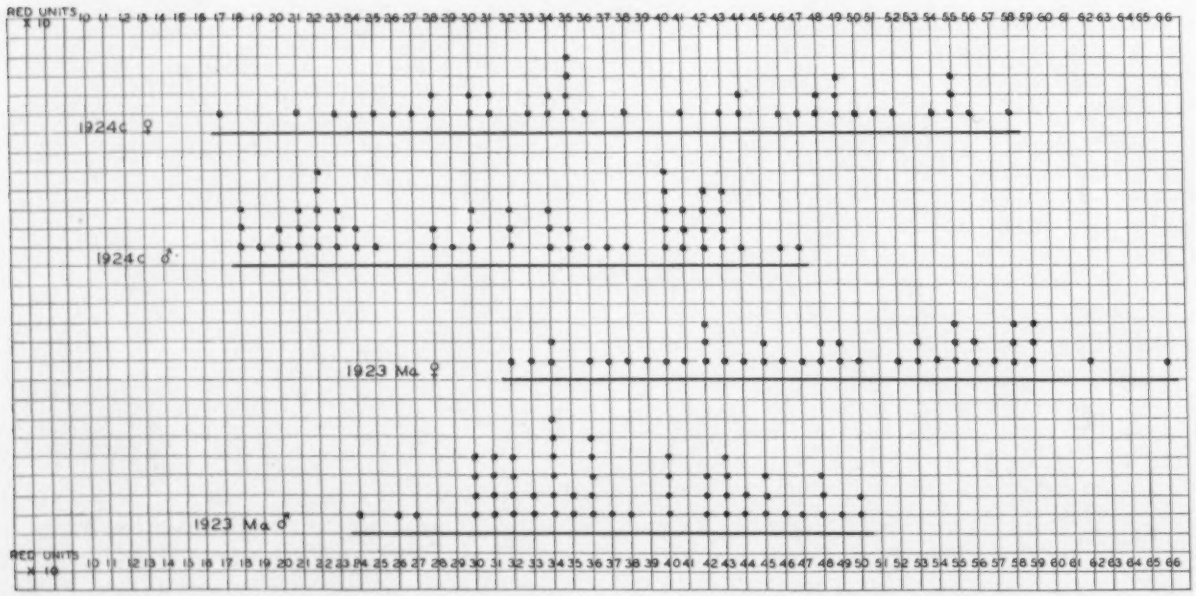

FIG. 8. Natural hybrid Kansas brood (1924c, August 16 – September 4) compared with a normal Kansas *eurytheme* brood (1923Ma, July 4 – August 1). Random sample of 1923Ma equal in number to 1924c. Distinctly visible orange begins here at about 10 in these Levibond units × 10.

Natural Hybrid Brood, Kansas Stock

Even casual inspection of one brood from a wild female *eurytheme* from Manhattan, Kansas, strikingly suggests natural hybridization with the local *philodice*, for no such extreme variability was seen in the other brilliant orange summer broods of *eurytheme* of Kansas, Colorado, and Arizona stocks. That such hybridization[9] in Kansas is probably rare is indicated by the fact that the two reciprocal *eurytheme-philodice* cross-matings, which with difficulty I succeeded in getting with Kansas stocks, were both sterile.

In this Kansas brood, 1924c (figs. 7, 8; table 1), the female range of variation measures nearly or quite twice that of the Arizona broods. It is 4.1 (5.8 to 1.7) (*cf.* only 2.5 and less in the Arizona broods (fig. 2) and 3.4 (between 6.6 and 3.2) in another large and brilliant Kansas brood, 1923Ma). The females of 1924c at the upper end of the scale, 5.8, exceed in intensity of red any individual in the Arizona broods; in Ma, in two females, it runs even higher (6.6). The striking and extraordinary thing about both sexes in 1924c is the paleness in red at the lower end of the scale. More than one-third of the females (viz 13) are paler than any of the females of Ma. Precisely the same is true of the males; 17 of the 56 are paler than any in Ma. The minimum in red, 1.7 in females, 1.8 in males, is far below that in any Arizona summer brood (fig. 2), none of which is below 2.2 and 2.6 even in the females.

The range in males of 1924c—2.9 (4.7–1.8) (fig. 8)—though much less than in the females (4.1), is not much wider than in Ma—2.6 (5.0–2.4). The widest range in any of the Arizona broods is 2.3 in 1913b. The nearest approach to this wide range is seen in the F_2 *eurytheme-philodice* hybrids, 1914g, in which the range of the male is 3.3 (4.1–0.8).

This variability in 1924c, obvious by casual inspection, is best expressed by the larger male and female coefficients of variation (28.5 percent and 28.7 percent), which are roughly twice those in the pure Arizona stock (12.7 percent and 15.36 percent) and about one-third larger than in the Kansas brood 1923Ma (17.8 percent and 18.4 percent). They stand nearest to the *eurytheme-philodice* back-crosses to *eurytheme*, which in the male were 31 ± 2.8 percent, 32 ± 4.6 percent, 34.3 ± 4.5 percent, and are exceeded only by the F_2 (*e. g.* 53.4 ± 11.5 percent in the ♂ and 40.4 ± 9.9 percent in the ♀ of 1914g). Thus 1924c most resembles a backcross between an F_1 hybrid, the presumptive father, and *eurytheme*, the mother.

Summary for the Kansas stock.—Eurytheme and its white female are common here, as are also *philodice* and its white female. In the former, no lethel gene associated with female whiteness was evident in the small sample of stock bred. Measurements of white females of *eurytheme* exceeded those of *philodice* in wing-spread, width of marginal band, and redness of central orange spot, with a few intermediates difficult to classify. A pale orange suffusion over white on the hind wings was seen in a majority of the white females in a brood of *eurytheme*.

Cross-matings both ways between the two species were obtained only with difficulty and with no observed evidence of fertility. However, the extreme heterozygosity in one of the *eurytheme* broods, seen in the wide range and high coefficient of variation in red, strongly points to previous hybridization, this being precisely comparable to a backcross to *eurytheme*. (Caterpillars of Kansas *eurytheme*, unlike those of Arizona and Colorado, are extraordinarily variable in color pattern, but these variations are independent of butterfly colors.)

Kansas *eurytheme* stocks readily mated *inter se* and produced abundant offspring. Kansas *philodice* females mated quickly with New Hampshire *philodice* males; a resulting brood was almost wholly female and showed dominance of the increased tendency toward red in western *philodice* and in *eriphyle*.

Nebraska Stock

Kearney, Nebraska, a little less than 200 miles northwest of Manhattan, Kansas, is in the valley of the Platte River, the south and north branches of which arise, respectively, just west of the Colorado and Wyoming localities from which my *eriphyle* stock came (map 1). It is not surprising that the yellow females of the Kearney stock resemble the mountain *eriphyle* a little more closely than do those of Kansas. The

[9] It had little to do with the extraordinarily variable caterpillar color markings that are peculiar to the Kansas *eurytheme* and were not observed in stock of that species from Arizona and Colorado. The irregular and possibly complex genetic basis of these larval characters studied in 1923 has not been described nor fully analyzed; 1923Ma, relatively homozygous for orange wing-color, was extremely variable in larval colors. In this respect 1924c was less variable.

MAP 1. Localities from which the butterfly stocks were obtained.

distances west from Kearney to the mountain stations, moreover, are about 350 miles by air.

The yellow female (mother of Na) from Kearney was caught by the Whitings on August 2, 1922, feeding and laying on alfalfa along with *eurytheme* (including one white female). My records show that it began to lay (white clover) August 8; eggs hatched August 13– ; first molt, August 16; second molt, August 20; first pupa, August 29; eclosion, September 5–31 (fig. 6). Three matings occurred, September 6–8, from which were obtained two broods, the eggs hatching September 18 and 26; the larvae died in attempted hibernation. No experiments in cross-mating were undertaken.

As is common in other *philodice*, the males of Na were slightly precocious: on September 5–7, 33 ♂♂ and 5 ♀♀ emerged; on the next two days, 28 ♀♀ and only 13 ♂♂. The total was: 90 ♂♂, 68 yellow ♀♀. These details agree closely with corresponding data for New Hampshire *philodice*.

BREEDING EXPERIMENTS WITH *eriphyle* AND *eurytheme*

Colorado Stock

Passing westward from the great plains of Kansas and Nebraska to the eastern side of the Rocky Mountains, we come to typical *eriphyle*. The yellow females all have strong traces of orange under the front wings, and a large proportion (September) have a flush of orange spread evenly over the upper surface of all the wings. The males lack orange above and are generally much smaller than the females.

The *eriphyle* stock came from a yellow female from Tolland, near Boulder in north central Colorado, a few miles west of Denver, through the kindness of the late Dr. Francis Ramaley. The female laid well (July 29 – August 14, 1915) on white clover, and the brood of 50 ♀♀ and only 13 ♂♂ emerged September 5 – October 14. There was no marked precocity of either sex. Arriving at Hanover from Tolland at the same

time were females of *C. eurytheme*, *C. alexandra*, and *C. scudderi*. The *eurytheme* ♀ laid profusely on alfalfa outdoors and produced during September a brood of 16 ♂♂ and 14 ♀♀, all brilliantly orange. They were larger than the *eriphyle* and were used for cross-mating experiments.

On September 10, 6 wild *philodice* ♂♂ (of Hanover, N. H.) were caged with 17 *eriphyle* ♀♀; four cross-matings quickly occurred. Two of the females were tested for fertility; one (eC[20]) laid fertile eggs on September 14–18, but the larvae (middle of October) were not successfully hibernated; the other female laid no eggs. On September 11 three other similar cross-matings occurred, the same *philodice* males in two cases mating again with other *eriphyle* females. At the same time four pairs of *eriphyle* were obtained. It is evident that *eriphyle* females mated as readily with these New Hampshire *philodice* males as with their own brothers and with some (50 percent?) fertility, one female being fertile, one sterile.

On September 15, 18 *eriphyle* ♀♀ flew for three hours with 11 *eurytheme* ♂♂; no mating occurred. On September 16, 17 *eriphyle* ♀♀ and 14 *eurytheme* ♂♂ spent two hours in the same cage on a hot, sunny day, with no mating. In another cage, 8 *eurytheme* ♀♀ and 9 *eriphyle* ♂♂ likewise failed to mate. On September 17, however, when 29 *eriphyle* (19 ♀♀ and 10 ♂♂) and 26 *eurytheme* (14 ♀♀ and 12 ♂♂) were caged together, three cross-matings did occur between *eriphyle* female and *eurytheme* male, one of which was fertile (the larvae died in hibernation); while another and probably the third were infertile; also there were two matings within *eriphyle* but none within *eurytheme*. The *eurytheme* females, failing to mate with their own kind on September 17, were given two other opportunities (September 22 and 23) to mate with *eriphyle* males but failed to do so.

In view of the numerous matings of *eriphyle* females (7 with New Hampshire *philodice*, 6 with their own brothers, and finally, after two days of unsuccessful trials, with 3 *eurytheme* ♂♂), it is remarkable that the *eurytheme* females did not mate at all. They were certainly fresh on the days of testing, September 16, 17, 22, and 23, for the period of eclosion of the brood was September 1–20. There was no collateral evidence that they were sterile.

Their sexual apathy with their own race interfered with discovering whether size difference between *eurytheme* and *eriphyle* tends to keep them apart. The reciprocal combinations are unlike as to congruity or incongruity in size of partners in cross-mating. That involving *eurytheme* female includes the greater size-incongruity and the smaller male. Since the male in any couple carries the female as a passive dead weight, this, *a priori*, would tend to make copulation in this particular combination difficult. Twelve of these *eurytheme* ♀♀ in wing expanse measured from $2\frac{1}{8}$ to $2\frac{1}{4}$ inches (av. 2.11),[10] while six (eC) *eriphyle* ♂♂ measured from $1\frac{1}{2}$ to $1\frac{11}{16}$ inches (av. 1.59).

In the reciprocal combination, *eriphyle* ♀ × *eurytheme* ♂, on the other hand, the size difference was less: 13 *eriphyle* ♀♀ varied between $1\frac{3}{4}$ and $1\frac{7}{8}$ inches (av. 1.72), 13 *eurytheme* ♂♂ ranged from $1\frac{3}{4}$ to $2\frac{3}{16}$ inches (av. 1.91). The fertile pair, *eriphyle*, eC[52] ♀ × eu[3] ♂, were respectively $1\frac{11}{16}$ and $1\frac{7}{8}$ inches, the *eurytheme* ♂ being only $\frac{3}{16}$ inch larger.

Aside from the fact that a fertile cross was made between these two very different Colorado stocks, the next most interesting fact was the extraordinary excess of females in the original *eriphyle* brood. A similar excess of *males* in *philodice* is not unusual in any brood attacked by wilt or other disease; the males, usually precocious, come through to maturity in larger numbers. This 80 percent of femaleness,[11] without female precocity, is an interesting physiological phenomenon which I have never observed in eastern *philodice*.

Also the increasing amount of red in the *philodice-eriphyle* complex, seen in passing westward from the plains into the Colorado mountains only about 300 miles, is of interest. The difference between the two races is evident in the females (fig. 6). On the upper side of the wings, the faint orange in Nebraska which barely touches red (1.1, 1.2) is shifted in a large proportion of the Colorado females to a clearly visible flush (1.2–1.4); a similar shift toward red is seen also on the under side of the front wings. The males show no clearly visible orange.

Wyoming Stock

Centennial, Wyoming, is roughly 110 miles north of Tolland, Colorado, and on the same

[10] A single *eurytheme* ♀, much smaller than her sisters and so not included with the other 12, measured $1\frac{5}{8}$ inches, the size of an average ♂.

[11] Note the similar sex ratio in "eKa," a cross between Kansas *philodice-eriphyle* ♀ × New Hampshire *philodice* ♂.

(eastern) side of Medicine Bow and Front Ranges of the Rocky Mountains. The altitude is about 8,000 feet.

Drs. P. W. and Anna R. Whiting on August 14, 1922, found *eriphyle* common in the meadows, laying on vetches and lupines. They saw no white females, no *eurytheme*. Males of *eriphyle* were in great excess.[12] Nine *eriphyle* females came through to Hanover alive, three of which, set over white clover, were laying from August 22 on, during the last week of August. The offspring of two of them all stopped feeding as half-grown larvae[13] and were dormant through September, October, and November; while Kansas *eurytheme* caterpillars in the same room, from eggs laid October 27–28 and hatched November 3– , were actively feeding. A third *eriphyle* female of the same lot from Centennial, however, simultaneously produced larvae, of which some showed no tendency to fast and lie dormant. These began to pupate September 22 and emerged during October (fig. 7, Wa, 22 ♂♂ and 2 ♀♀). The other caterpillars of this brood (Wa) were put into hibernation in November and taken out April 14; 14 survived. Pupation began May 1; 3 ♂♂ emerged May 8–10, and a ♀ May 11. This female, mating with a brother, produced a large summer brood (Wb, 85 ♂♂, 95 ♀♀, June 22 – July 9, 1923). Numerous unsuccessful attempts were made during more than a week early in July to get sister-brother matings within this brood and also to mate the females with New Hampshire *philodice* males. Two Kansas *eurytheme* males ("Ma" brood) were likewise unsuccessful. Ovaries of the Wb females dissected showed only immature ova.

Seasonal variations, Wyoming males.—Size difference between these males of the late fall - early spring generation and those of the early summer were not conspicuous; in general, the former were slightly smaller in wing-spread, and both sexes in each generation were smaller than in *philodice*, *e. g.*, of Nebraska and New Hampshire.

The black marginal band in males, in general, was narrower in the fall-spring than in the summer generation, and, in some males, it was crenated along its inner edge by incisions of yellow ground color following the veins outward. This seasonal narrowness occurs also in *philodice;* the band in summer males of *eriphyle* in Wyoming appears to be relatively wider than in *philodice*. The central spot of the hind wings of the male, in this stock, varied from deep orange to pale yellow. Among the fall generation of 22, roughly in 11 it was bright orange, in 7 intermediate, and in 4 faint; in one of these it was nearly yellow like the ground color. Inspection of the summer brood gave a tentative count of 15 bright orange, 20 intermediate (pale orange), and 12 yellow, with definite correlation between large size and intensity of orange, though with certain exceptions. In some males the spot was extraordinarily small.

The melanic pigmentation of the under-surface scales, not pronounced in this particular stock, is sharply contrasted with the clear pale-orange under surface of the hind-wing in the summer generation, which measured 1.8–2.0 units of red in the few counts made.

Wyoming females.—Only two of the four females of the fall-spring generation are in condition for precise examination. They appear smaller than most females of the summer brood, though the wing-spread ($1\frac{5}{8}$ inches) is about the average in that brood. This illusion is due to the narrowness of the front wing, $\frac{1}{2}$ inch vs. $\frac{5}{8}$ inch in width. The width of the hind wing, $\frac{5}{8}$ inch, is exceeded by many but not all of the summer females.

One of the two October females has the wing-color pattern of both mothers, viz, hind wing almost devoid of black border and with a bright-orange central spot. This pattern is reproduced in some of the summer females, but the most of the latter have more than a vestige of a black hind-wing border; in which respect they resemble the second October female, which, however, differs from all the others in being strongly melanic above as well as below. The hind wings, especially, are suffused with black scales interrupted only by 6 submarginal spots on each wing lacking them and by the large, bright-orange central spot.

The upper-side ground color and the under-side orange of the front wing are apparently not much subject to seasonal change, for these October females measure 1.1 and 1.2 in red above; 2.0 and 2.3 below. The mode in the summer brood (fig. 6) is 1.1 above and 2.2 below.

As in the males, the hind-wing central spot of summer females varies from bright orange to a paleness which matches the yellow ground color

[12] At higher altitudes also, a few males of *eriphyle* were seen. Dr. Klots informs me that both *eriphyle* and *eurytheme* occur commonly in meadows above Centennial at 10,000 to 12,000 feet altitude, and hence probably are to be found at Centennial and lower levels.

[13] Perished underground in hibernation.

itself. Among the 67 summer females measured for ground color by Dr. Croasdale, she classed the central-spot colors (which are not easily measured for redness) as bright orange in 22, medium orange in 25, pale orange and clear yellow in 20.

The central spot in both the grandmother from Wyoming and the mother in the May brood is bright orange. Whether the latter mated with the brother in which it is bright orange, or with one of the other two in which it is medium orange, is uncertain, for to make sure of a mating all three males were caged with her over the food-plant, a method not to be recommended except in a real emergency.

Alberta Stock

From Midnapore (near Calgary), Alberta, through the kindness of the late H. Wolley Dod, I received on August 12, 1915, three live *eriphyle* females, and on August 16 three more. Two of these produced (eclosion between September 16 and October 16) broods of considerable size: 1eA consisted of 32 ♂♂, 16 ♀♀; 3eA of 26 ♂♂, 22 ♀♀. None of the nine ♀♀ sent to me by Mr. Dod (including three arriving dead) was white. He wrote me: "The only *Colias* common here besides *christina* is *eriphyle*. *Interior* is fairly common about 12 miles further west. *Eurytheme* has very occasionally been common, but is extremely erratic in appearance, probably migratory."

Unfortunately no mating experiments were recorded. The *eriphyle* stock from Colorado (eC), emerging during the same four weeks (and ten days earlier), required and received all available attention.

Oregon and California Stock

None of my breeding stocks came from these two states, the *Colias* population of which in relation to genetics and ecology is being exhaustively studied by William Hovanitz at the California Institute of Technology. I have little to add to what he may present.

Mrs. Agnes M. Veazie, of Portland, Oregon, in 1916–17 wrote me that in northern Oregon three forms of "*eurytheme*" occur: "full orange, yellow laved with orange, and clear yellow. I notice no difference as to size in the three forms, nor do they seem to be seasonal." I received from her representative pairs of these three kinds caught September 13, 1917, at Gateway, Oregon. This is just east of the Warm Springs Indian Reservation, which lies northeast of Mount Jefferson of the Cascade Range. These specimens include, besides two pairs (including a white female) of typical *eurytheme*, three *eriphyle* (one ♂ and two ♀♀). The fresher of the *eriphyle* females (the other being faded) closely resembles in details of upper-side coloration the palest of my Alberta *eriphyle*, 3eA[33] ♀ (fig. 7), which measures 0.7 in its red component. The male, in narrowness of black border and sharp-pointedness of front wing, is closely like some of the males of the Alberta brood.

Similar to the others in size and yellow ground color is a pair far more like *eriphyle* than like the brilliant summer *eurytheme*, but with a faint orange flush near the inner (posterior) margin of the forewings and still more faintly expressed on the hind wings. There are two reasons for judging that these are hybrids and not *eriphyle*. (1) In such *eriphyle* females as are orange-tinted, the orange is spread evenly over the whole upper surface and is more intense on the under surface of the forewing; in this female, however, it is concentrated near the inner margin above and is paler on the lower surface. (2) The male in *eriphyle* is never orange. The orange of this male measures 1.7 in red, that of the female 2.0.

Dr. Hovanitz was so kind as to send me for examination some of his June, 1941, specimens from eastern California (Round Valley, southeast of Yosemite National Park), the colors of which were measured for me by Dr. Croasdale. Among the males only, six *eriphyle* measured from 0.5 to 0.8 in red, four *eurytheme* from 3.2 to 4.2, and six, which may be regarded as *eurytheme-eriphyle* hybrids, measured from 1.2 to 2.2. Two of these six intermediates (measuring 2.2 and 2.0) appear to be of an interspecific F_1; the other four are pale enough to be of a back-cross to *eriphyle*.

Summary

From the seasonally polymorphic orange *Colias eurytheme* of the Western States and Mississippi Valley, a yellow species-complex has originated, with which it occasionally, and in recent years more frequently, hybridizes. One of the two minor species of this complex is *C. eriphyle*, a far-western mountain race, geographically closest to *eurytheme*'s earlier habitat but still cut off by the Sierra Nevada Range from the California coast. Its summer females retain in varying degree diffuse traces of orange. The other minor

species is the clear yellow *C. philodice*, the more typical members of which have long occupied the Central and Eastern States; a transitional *philodice* (approaching *eriphyle*) is found in the Great Plains of Kansas and Nebraska. Mating experiments showed strong pairing affinity and fertility between the northeastern (New Hampshire) *philodice* and Kansas *philodice* (*eriphyle*). *Eriphyle* of the mountains, on the other hand, differed somewhat from the eastern *philodice* in breeding habits, in its smaller size, and (especially in the female) in color.

Invasion eastward across the Alleghenies by the vigorous orange species, begun about 1900, is now (since 1934) reaching New Hampshire. Its advent into a population of *philodice* is accompanied with natural hybridization. Hybrids, though still rare in the extreme northeast, are recognizable as F_1 or backcross individuals and occur in approximately the same numbers as pure *eurytheme*. About 1.5 percent of a *Colias* population (648) caught at Hanover, N. H., in 1940 were immigrants (*C. eurytheme* and *eurytheme-philodice* hybrids).

Mating experiments in 1913 and 1914 between *eurytheme* of Arizona and *philodice* of New Hampshire (fig. 1) showed less cross-mating proclivity in *eurytheme* male than in *philodice* male. In neither reciprocal cross was there noticeable sterility; four of the six F_1 broods were of fair or large size.

When a *philodice* male was the original parent, however, eight of the nine matings (1913) between two F_1 individuals were sterile. Male sterility was clearly indicated in two individuals, female sterility in one case; in four couples no facts are available as to which sex, if not both, was sterile.

A small majority (4 in 7) of the backcross matings between F_1 male and *eurytheme* female were fertile and produced numerous offspring.

F_1 hybrids from the original cross by *eurytheme* male in 1914 mated *inter se* readily; 10 pairs were quickly made. No extensive tests of fertility of the fecundated females were attempted, but the three tested showed only slight fertility; from them came F_2 families 1914e, f, and g (fig. 1 and pl. A), consisting respectively of 12, 2, and 34 imagines. The only F_2 brood of 1913, q, was also small; diminished fertility was indicated in all four of them.

Red (orange) is incompletely dominant, intermediate between the brilliant orange of *eurytheme* (in midsummer) and the clear yellow of *philodice* (pl. A, F_1). Expressed in Ridgway's code, it is roughly "apricot yellow," intermediate between the orange "cadmium yellow" and "picric yellow." "Apricot yellow" measures 2.7 in red, Levibond (fig. 2 and p. 411 of text).

The inhibitory action of climatic conditions is illustrated by F_1 broods 1913v and 1914d (fig. 2). In the former, emerging in December, the average in red was reduced from 2.2 or 2.5 of summer ♂♂ to 1.24, *i. e.*, slightly above clear yellow, and the range in red variation was exceedingly narrow.

The small F_2 broods (October) have a wider range and a much greater coefficient of variation than the F_1, even than those showing maximum midsummer variability. They include roughly 25 percent of clear yellow individuals (pl. A, F_2). Seasonal conditions uniformly reduce, or intensify, the orange coloration in an F_2 series without interfering with the segregating effect of the genes for red-yellow. The brightest F_2 ♂♂ (October) reached only the average intensity of *eurytheme* ♂♂ of July–August.

In the backcross to *philodice* (pl. B), there was in both sexes a pronounced segregation into two groups: yellow and pale orange, with a decided gap between them, especially in the ♂. These groups were equal in the ♂, as would be expected, but in the ♀ the orange heterozygotes were nearly three times as numerous as the yellow recessives.

The November–December backcrosses of F_1 females to *eurytheme* males (fig. 2) extend into red only to the *eurytheme* ♀ summer average, which is slightly below the *eurytheme* ♂ summer average. At the other (paler) end of the scale of redness, they extend slightly beyond the limits of clearly visible orange. About 25 percent are similar to the pale orange "*ariadne*," and 75 percent to the intermediate orange "*keewaydin*" —names applied by collectors to seasonal forms of *eurytheme* formerly regarded as species. These broods gave skew curves, with most of the individuals near the yellow end of the range, gradually trailing off into orange.

Summer F_1 broods (fig. 2, 1913o, 1914a, etc.) have a male average in red numerically twice as high as one emerged in December (F_2, 1913v). Melanic pigmentation (under side of wings), on the contrary, had a winter male average 6.5 times that of the summer F_1, and in the females it was 5 times as intense.

In late-fall backcrosses (fig. 2) and winter offspring of two heterozygotes, intensity of red is

also scaled down to levels far below genetic expectation, in spite of fairly high greenhouse temperatures.

On the assumption that amount of sunlight and length of day may control the rapidity of feeding and affect the processes of metabolism immediately determining pigmentation and size, the outdoor winter conditions in Louisiana are considered. There, winter *eurytheme* is even smaller and paler than the specimens raised under the northern greenhouse conditions, and yet no such shortness of day or lack of sunlight exist as in the north.

Probably the condition of the food-plant after the frosts or extreme cold begin, south or north, is a very important factor in restricting the growth of the larva and determining the small size and pale orange color of the butterfly.

Experiments with eriphyle.—Measurements of the varying tinge of red in the yellow *females* of *philodice-eriphyle* broods raised in 1915–16 and 1922–24 (fig. 6) show a gradual increase in intensity geographically from the plains of Kansas and Nebraska through the mountain meadows of Colorado and Wyoming to Alberta. The males, however, are invariably clear yellow, and the slight increase in the red component in Wyoming and Alberta *eriphyle* is not conspicuous. Orange under the forewings, characteristic of the female *eriphyle*, is regularly stronger in red than that of the upper surface, and increases gradually from the Kansas and Nebraska broods through those of Colorado to those of Wyoming and Alberta. In the male the corresponding wing area is pale yellow, almost white.

White females of Kansas *philodice* (*eriphyle*) differed in general from those of *eurytheme* in size, width of marginal black band, and redness of central orange spot. Kansas *eurytheme* broods were prolific; but matings between this species and Kansas *philodice* (*eriphyle*) were made with difficulty and with no observed evidence of fertility, in marked contrast to Kansas *philodice* ♀ × New Hampshire *philodice* ♂, which mated readily and with fertility, though the brood produced was nearly 82 percent female. However, one wild Kansas *eurytheme* ♀ produced a definitely hybrid brood (fig. 8), evidently from having mated with an F_1 *eurytheme-philodice* ♂.

Nebraska broods of *philodice* (*eriphyle*), aside from the points already noted, resembled physiologically those of New Hampshire *philodice*.

Colorado *eriphyle* females, of a brood 80 percent female, mated readily with New Hampshire *philodice* males, with some fertility; a fertile cross by a large *eurytheme* male was obtained. The *eurytheme* females failed to mate either with their own kind or with the (small) *eriphyle* males. The *eurytheme* brood had been raised outdoors on alfalfa, the *eriphyle* in the greenhouse on white clover (eclosion in September).

Wyoming *eriphyle* caterpillars of two broods showed a strong tendency to fast and go into hibernation early (September), but a third brood was purposely split into two parts; some emerging in October were mostly males, while others hibernating resulted in May in one female and three males. The female, mated with a brother, produced a large early-summer brood (fig. 7, Wb), in which females were slightly in excess and apparently sterile, for no mating occurred with *eriphyle*, *eurytheme*, or New Hampshire *philodice* males. The ovaries examined were immature (early July).

The Alberta *eriphyle* came from a locality where *eurytheme* was rare. Two broods emerging late in the season (September 16 – October 16) were normal (*cf. philodice*) in their excess of males, which were smaller than those of New Hampshire *philodice;* the tips of the forewings were in general more pointed, the black border was relatively wider, and the central hind-wing spot was deeper orange (compared with *philodice* males of the 1940 September survey). In general, these are indications of affinity with *eurytheme*.

Oregon and California stock.—Specimens of both sexes from northern Oregon and of males from eastern California strongly indicate, in both size and color measurements, the occurrence in those regions of some, and rather common, natural hybridization between *eriphyle* and *eurytheme*. Summer males such as these, faintly flushed with orange, are not to be regarded as *eriphyle* but as *eurytheme-eriphyle* hybrids.

Eriphyle, notwithstanding pronounced traces of orange in the female, is an independent, true-breeding species, not a seasonal or other "form" of *eurytheme*, as frequently has been claimed. That it and *philodice*, into which it merges on the Great Plains east of the Rocky Mountains, have been evolved from *eurytheme*, is in the highest degree probable.

References

BROWER, A. E. 1929. *Eurymus eurytheme* Bdv. (Lepid.) at Ithaca, N. Y. *Jour. New York Entom. Soc.* **37**: 437.

CLARK, A. H. 1925. Some unusual and interesting butterflies from eastern Massachusetts. *Psyche* **32** (6): 293–298.

——. 1932. The butterflies of the District of Columbia and vicinity. *U. S. Nat. Mus. Bull.* 157: 1–156, 32 pl.

COMSTOCK, J. A. 1927. Butterflies of California. Los Angeles: 334 pp., 63 pl.

EDWARDS, W. H. 1868–1897. The butterflies of North America. Boston and New York. (Series 2, 1884, *Colias* II, III, pl. 3, fig. 1; series 3, 1897, *Colias* III.)

——. 1876. Description of new species of diurnal Lepidoptera found within the United States and British N. A. *Trans. Am. Entom. Soc.* **5**: 202–208.

——. 1884. Notes upon a small collection of butterflies, made in Judith Mtns., Montana, in 1883, by Wm. M. Courtis, M.E. *Papilio* **3** (7/10): 157–164, "1883."

——. 1887*a*. On the position of *Colias Hagenii* Edw. *Canadian Entomologist* **19**: 170–175.

——. 1887*b*. On *Colias Eriphyle* Edw. and *C. Hagenii* Edw. *Canadian Entomologist* **19**: 218–220.

FIELD, W. D. 1938. A manual of the butterflies and skippers of Kansas (Lepidoptera, Rhopalocera). *Bull. Univ. Kansas, Biol. Ser.* **39** (10): 1–328, 2 pl.

GEROULD, J. H. 1911. Suggestions as to the culture of butterflies. *Science* **33** (843): 307–310.

——. 1913. Heredity in butterflies. *Carnegie Inst. Washington Year Book* 12: 113–114.

——. 1914. Species-building by hybridization and mutation. *Am. Naturalist* **48**: 321–338.

——. 1923. Inheritance of white wing color, a sex-limited (sex-controlled) variation in yellow pierid butterflies. *Genetics* **8** (6): 495–551.

——. 1941. Genetics of butterflies (*Colias* spp.). (Abstract.) *Genetics* **26**: 152.

GUNDER, J. D. 1924. Several new aberrant Lepidoptera (Rhopalocera) from California. *Entom. News* **35** (5): 153–158.

HOLLAND, W. J. 1910. The butterfly book. New York: xx + 382, 48 pl.

KLOTS, A. B. 1929. Notes and additions for 1928 to the New York State list (Lepidoptera). *Jour. New York Entom. Soc.* **37**: 41–42.

MAY, H. 1894. Ueber *Colias chrysotheme* Esp. *Jahresber. Wiener entom. Ver.* **5**: 1–6, 1 pl.

NAPIER, A. H. 1924. *Colias eurytheme*—first recorded in Philadelphia, Pennsylvania. *Entom. News* **35** (5): 176–178.

NEEDHAM, J. G., AND OTHERS. 1937. Culture methods for invertebrate animals. Ithaca: 590 pp. (See pp. 365–368.)

ONSLOW, H. 1919. Inheritance of wing colour in Lepidoptera. I. *Abraxas grossulariata* var. *lutea* (Cockerell). *Jour. Genetics* **8** (4): 209–258. ("Tintometer" described on pp. 211–214.)

SCUDDER, S. H. 1889. The butterflies of the Eastern United States and Canada. 3 v. Cambridge: 1958 pp., 89 pl., 3 maps.

——. 1899. Brief guide to the commoner butterflies of the Northern United States and Canada. New York: 1–210, 22 pl.

WATSON, F. E. 1929. *Eurymus eurytheme* f. *amphidusa* f. ♀ *pallida* Cockerell. *Jour. New York Entom. Soc.* **37**: 48.

WRIGHT, W. G. 1906. The butterflies of the west coast of the United States. Second ed. San Bernardino: 257 pp., 32 pl.

LIFE ACTIVITIES OF FORAMINIFERA IN RELATION TO MARINE ECOLOGY

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ABSTRACT

The number of chambers in the test of a foraminifer is indicative of the degree of maturity of the individual, and the rate of growth can be determined from the mean number of chambers in a series of samples of a population. The presence of juveniles in a sample and cytological evidence of gametogenesis suggest periods of reproduction. From the number of generations produced annually, the number of individuals asexually produced as determined from cultures, and the ratio of microspheric to megalospheric individuals on the floor of the sea, it is possible to estimate the productivity of a species. The rate of mortality from various causes and at different seasons can be estimated from the number of living Foraminifera per unit area on the floor of the sea. When these data are correlated with data concerning measurable ecological conditions in the sea, it is possible to evaluate the relative importance of these and other conditions on the success of a species. When frequency-distribution curves for growth stages in populations, taken in a region where the conditions affecting growth and reproduction have been studied, are compared with similar curves for samples of populations taken in a region where measurements of these conditions have not been made, much may be deduced concerning the possible seasonal variations in these conditions in the second region. *Elphidium crispum* (Linnaeus) was used in this work, and the conditions discussed include food, bottom, depth, temperature, salinity, pH, oxygen tension, turbulence, turbidity, animal associates, parasites, and enemies. Series of samples were taken in the vicinity of Plymouth, England; Nice, France; Batavia, Java; and La Jolla, California.

INTRODUCTION

THE basis for interpretative work in paleoecology is knowledge of those conditions which are essential to the success of species similar to those observed in fossiliferous deposits. The persistent nature of the calcareous tests of the Foraminifera, their universal distribution in marine sediments, both recent and geological, and the notable effect of slight differences in ecological conditions upon the species in populations make them a useful guide to the biotic conditions that existed in ancient seas. Thus far, papers on the ecology of the Foraminifera have consisted of descriptions of assemblages of presumably empty tests, and the only chemical and physical conditions in the sea that have received more than a passing comment have been temperature, depth, salinity, and bottom sediments (see Vaughan, 1940, and Ladd, 1941).

In our study of the productivity of the Foraminifera in the sea (Myers, 1942*a*), the life span, rate of growth, rate of reproduction, population per unit area, and the rate at which the tests are contributed to the sediments were discussed. In the present paper we shall attempt to correlate these data with measurable ecological conditions in the sea, including temperature, salinity, oxygen tension, pH, illumination, and the nutrient salt content of the water as well as the influence of a varying food supply upon growth and test morphology, the effect of the substratum upon distribution, and the importance of animal associates, parasites, and other enemies.

Further and more exact laboratory experiments would have contributed additional infor-

mation concerning the limits of tolerance of the Foraminifera for certain ecological conditions, but could only have supplemented the interpretation of the observed effect of these variable conditions acting simultaneously upon the several phases of the life cycle. Our purpose in this and the preceding paper has not been to make arbitrary statements where the evidence did not warrant, but rather to present observations and suggest methods that would contribute to a better understanding of the role of the Foraminifera in the economy of the sea.

Material and Methods

Elphidium crispum (Linnaeus) was used for the quantitative study of the productivity of the Foraminifera referred to above. The present paper makes use of the same data in an attempt to explain the influence of ecological conditions in the sea upon the life activities of the same species.

When individuals of *E. crispum* are killed, hardened, decalcified, stained, and cleared, it is possible to distinguish those that were feeding actively, were about to reproduce, or were in a dormant condition. When chamber counts for samples of populations taken monthly for twelve months and numbering from 500 to 1,000 individuals are plotted as percentage frequency-distribution polygons, much may be learned concerning the rate of growth, the life span, the periods of reproduction, and the influence of ecological conditions upon the life activities (see plate I, figs. 1 and 10).

In the life cycle of *E. crispum* there is an orderly succession of sexual and asexual generations. This alternation of generations results in microspheric individuals having a minute initial chamber and megalospheric individuals in which the initial chamber is relatively enormous. Microspheric agamonts asexually produce megalospheric gamonts, which in turn give rise to biflagellated gametes. The union of pairs of gametes in fertilization results in zygotic amoebulae that develop into microspheric agamonts. Reproduction terminates the life of the individual because all of the protoplasm and much of the calcium carbonate in the test is utilized in the production of the new generation or the gametes, as the case may be. The sexual phase of the life cycle is least successful as regards the number of progeny produced, with the result that during much of the year the ratio of sexually produced microspheric to asexually produced megalospheric individuals living in tide pools is only about 1:25, while below low-tide level the ratio is 1:40 or even 1:50. Immediately after sexual reproduction by megalospheric gamonts in the spring, ratios as low as 1:1 have been observed. The former ratios are again restored following asexual reproduction by the microspheric agamonts (Myers, 1942*a*).

Much of the material for this and the preceding paper was taken within Plymouth Sound, on the southwestern coast of England, where the average depth does not exceed 30 feet and the extreme tidal range is 16 feet (fig. 1). Several streams

Fig. 1. Map of Plymouth Sound showing the position of the stations referred to in the text.

with wide estuaries empty into the sound, and during periods of heavy rainfall these affect the salinity, particularly at the surface, where it varies with each tidal phase, and from season to season. The estuaries and the main channel have mud bottoms, while on either side of the main channel where the Foraminifera are most numerous, the bottom is covered with quartz sand and fine shell gravel. The abrupt rocky shores are fringed with dense growths of *Fucus*, *Laminaria*, and other algae, and tide pools on the shelving reefs usually contain dense growths of *Corallina*. The region supports a rich and varied macrofauna and microfauna, including the densest population of *E. crispum* we have ob-

served in any sea or ocean. Additional material from the English Channel in the vicinity of Plymouth Sound as well as material from the north coast of the Mediterranean Sea, the western end of the Java Sea, and the Pacific coast of California will be discussed.

The methods used for collecting and preparing the Foraminifera for study have been amply described (Myers, 1942*a*), and for that reason will not be repeated here.

In dealing with populations of larger invertebrates such as mollusks, echinoderms, and arthropods, migrations and the segregation of age groups according to depth or other conditions are often confusing (Moore, 1938–1939). In the Foraminifera the rate of movement is too slow to account for any of the changes in populations discussed, for when sediments or washings from algae containing *E. crispum* are placed in an aquarium, the more active individuals work to the surface of the sediments and up the walls to a height of 9 to 12 cm. in 12 hours. This movement is mainly in one direction and probably approaches the maximum rate at which these organisms are capable of moving over the floor of the sea. One of these Foraminifera moving continuously at this rate for one month would traverse a distance of only 7.2 meters. In one region we obtained samples of a population of *E. crispum* that had been sorted according to size as a result of winter turbulence and current action, but such an occurrence is unusual.

Food of the Foraminifera

The Foraminifera, in common with other free-living rhizopods, are holozoic, that is, they depend upon particulate food for sustenance. Cytoplasmic inclusions in the terminal and adjacent chambers in the majority of benthonic species living in shallow water consist for the most part of unicellular plants derived from the substratum, and to a lesser extent the phytoplankton in the overlying water. Diatoms are the most numerous and readily identifiable inclusions, although soft-bodied flagellated organisms, including the gametes of larger algae, filamentous algae, minute eggs, and cysts, are also recognizable. Feeding experiments and the rare inclusion of an appendage of a minute arthropod in the distal chamber of a test suggest that the Foraminifera digest animal tissue by means of ferments carried in the pseudopodia; and in Foraminifera in which the aperture of the test will admit sizable particles, digestion continues after the food has been ingested. Although most Foraminifera readily accept animal tissue as food, those which we have studied, including larger species found only in tropical waters, seem incapable of capturing the smallest ciliate or the minute nauplii of arthropods that become entangled in the filose and anastomosing pseudopodia when zoöplankton is added to well-established cultures in which the Foraminifera are actively feeding upon other organisms. Therefore it would appear that the main sources of animal proteins available to the Foraminifera consist of dead organisms or the residual protoplasm contained in sloughs and exoskeletons (pl. I).

The pseudopodia of *E. crispum* are attenuated to the vanishing point except when viewed under the highest powers of the microscope, and it is exceedingly doubtful whether this species captures organisms capable of offering more than passive resistance. Because of the small diameter of the apertures of the test, the only recognizable food inclusions are soft-bodied organisms, presumably the gametes of algae (Lister, 1895; Føyn, 1936) and minute fragments of diatom frustules. Material recently removed from the sea often contains tests of *E. crispum* to which are attached masses of ectoplasm in which are enmeshed numbers of minute organisms and bits of organic debris upon which the Foraminifera were probably feeding—a condition that was most conspicuous during the spring outburst of phytoplankton production. Although we have less direct evidence as to the nature of the food of *E. crispum* than we have for species in which entire organisms are ingested, it seems evident that the food of this species, in common with other Foraminifera, includes both micro plants and animals, either living or dead, and derived both from the water and from the substratum upon which they live.

Before we consider the possible influence of other ecological conditions upon the life activities of the Foraminifera in the sea, it is necessary to consider the probable effect of the seasonal distribution of food organisms upon growth and reproduction. For a discussion of the food of the Foraminifera, see Jepps (1926), Calvez (1938), Føyn (1936), and Myers (1935, 1936, 1940, and 1942*a*).

Food Cycle of the Foraminifera in the Sea

Foraminifera as well as other animals living in the sea depend directly or indirectly upon the utilization of nutrient salts by plants. For a

time these salts are bound up in the substance of the plants and the animals that eat them, but they are again restored to the water following death and bacterial decomposition. In the vicinity of Plymouth Sound the maximum concentration of nutrient salts is to be found in the early spring, and with the lengthening hours of sunlight in March there occurs an outburst of photosynthetic organisms, principally diatoms, which rapidly reduce the concentration of these salts, so that by June the available supply of nitrates is largely depleted, and there is almost a complete absence of soluble phosphates (fig. 2). Where the depth of the water does not exceed that of the photic zone, there develops on the bottom a microflora, the productivity of which is controlled by the same conditions that limit the productivity of the phytoplankton, and along the shore these same conditions also determine the rate of growth and reproduction in the larger algae whose spores are used as food by the Foraminifera. The spring crop of phytoplankton soon depletes the nutrient salt content of the water, and in turn the phytoplankton is depleted by a rapidly increasing population of herbivores, whose consumption of these plant cells is more dependent upon the number of cells available than upon the actual requirements of the animals, since the number of faecal pellets observed in the water bears a closer relationship to the number of diatoms in the sea than to the zoöplankton population. These faecal pellets, rich in nutrient salts, provide a suitable substratum for the growth of bacteria, and at depths appreciably below the photic zone these faecal pellets and their bacterial flora probably constitute an important source of food for the Foraminifera.

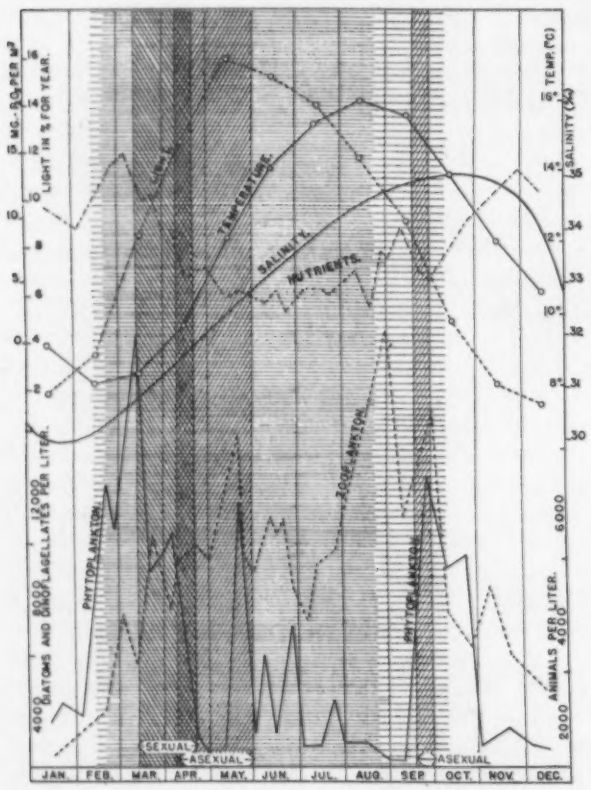


FIG. 2. Ecological conditions in the sea in relation to growth and reproduction in *Elphidium crispum* living on a sandy bottom 9 meters below low-tide level. The curve for nutrient salts based on the P_2O_5 content of the water would roughly parallel curves for NO_3 and SiO_2, and the curves for plankton organisms show the abundance of individuals but do not take into account the numbers produced or utilized by plankton feeders. Growth and reproduction in the Foraminifera as indicated by shading were most pronounced in the spring when food was abundant and at a time when other conditions might be considered least favorable, and under conditions that except for food were vastly different from those which induced reproduction in the fall. In the late fall conditions related to storm-induced turbulence greatly reduced the activity of the Foraminifera, while food was still abundant and other conditions seemed favorable for further growth.

After the spring outburst of phytoplankton there are several minor summer outbursts, and a longer and less intense fall outburst, which is limited by the decreasing hours of sunlight as winter approaches. The abrupt decline in the phytoplankton population in the spring does not result in a corresponding reduction in the numbers of plankton animals, so that variations in the zoöplankton populations are neither so frequent nor so intense. Temperature seems to have slight influence upon phytoplankton production, for February and March, the months of greatest abundance, include the period of lowest water temperatures in the sea, while in September and October, the months that are second in abundance, the water is only slightly colder than in August, the warmest month in the year. For references and a more complete discussion of plankton production in the sea, see Harvey et al. (1935).

The plankton cycle within Plymouth Sound is influenced by somewhat wider fluctuations in hydrographic conditions than in the English Channel opposite Plymouth, where the data for figure 2 were obtained; but from the available data and the amount of water exchange, it is evident that the dominant features, including a spring and fall

outburst of phytoplankton production and a more gradual increase in the zoöplankton, beginning in the spring and reaching maximum in the early fall, are similar in the two areas. The time and intensity of these outbursts vary somewhat from year to year, and the curves presented in figure 2 should be considered with this in mind.

Influence of Food upon Growth and Test Morphology

In Plymouth Sound the diameter of the proloculus of microspheric tests in samples taken from tide pools ranges from 6μ to 16μ, while those taken in the sublittoral zone range from 6μ to 19μ. The diameter of the proloculus of megalospheric tests from these life zones is 28μ to 73μ and 54μ to 125μ, respectively. The rate at which chambers are added to the tests depends upon the need for growth that results when food is consumed in excess of the basic requirements of the organisms. When adequate food is available, growth is continuous; therefore the number of chambers produced is related to the duration of the period when sufficient food is available to induce growth. The mean number of chambers produced by microspheric agamonts in the littoral and sublittoral zones during the first growing year was 29 and 48, respectively, while in megalospheric gamonts it was 21 and 34. This amounts to 40 percent more chambers and a 60 percent larger test for individuals produced in the sublittoral zone compared with those from the littoral zone—a difference that had persisted from the earliest developmental stage (figs. 3 and 5, and Myers, 1942*a*).

It might be argued that these two groups of *E. crispum* which are similar morphologically are dissimilar physiologically as a result of genetic differences. This could be demonstrated by maintaining cultures of pure strains of *E. crispum* for several generations under controlled conditions. However, it is obvious that growth is greatest where food is most abundant and where feeding activities are not interrupted by adverse conditions that result from surf and tidal changes.

The tests of *E. crispum* also vary in shape, depending upon the ecological conditions under which they are produced (fig. 4). In the spring, when food is abundant, the chambers added to the test are longer, narrower, and thinner than those added the previous year, especially in the late fall, when food is relatively sparse. For this reason there is often an abrupt break in the series of chambers, which results in the test having a notched keel (fig. 4*C*). Variations in the length of the chambers are most noticeable in the protoplasmic casts of the Foraminifera, and these were used in determining the rate at which chambers are added to the tests in the early months of the second year.

The maximum rate of growth and the largest tests were produced in the western part of Plymouth Sound below the Jenny Cliffs, the second largest opposite Drake's Island, and the smallest opposite the town of Cawsand, where conditions were least favorable (fig. 1). When the rate of growth is retarded, the test is thicker and more circular in outline (fig. 4*B*), while rapid growth results in a decidedly thinner test, a more distinct keel, and a terminal chamber having a longer apertural face (fig. 4*A*). This thinner type of test was the only one produced in the vicinity of Drake's Island in 1939, while thicker tests from less favorable years were numerous in the surface sediments of this area. In tropical regions, where the rate of growth is somewhat less but more continuous, the tests of this and related

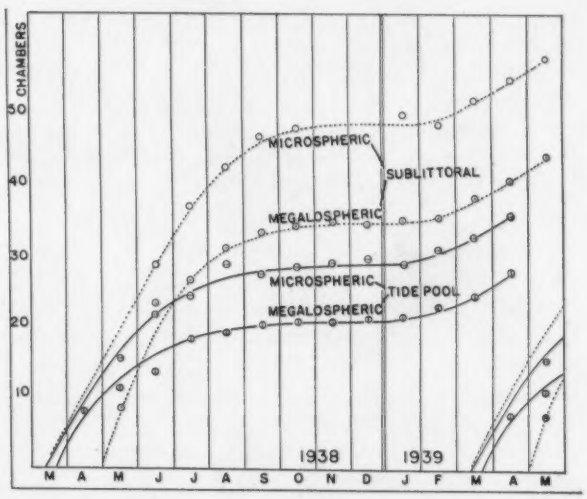


Fig. 3. Rate of growth in *Elphidium crispum*. Entire lines represent tide-pool populations, and dotted lines populations in the sublittoral zone. Growth during the first year is based on the mean number of chambers in the samples and for the spring of the second year on the mean number of chambers added to larger tests since reproduction by larger individuals tends to reduce the mean size. Sexual reproduction as determined from cytological evidence of gametogenesis began at about the same time in both life zones. Asexual reproduction in tide pools began about 1 week later and below low-tide level about 5 weeks after that. Forty percent more chambers and a 60 percent larger test were produced in the sublittoral zone.

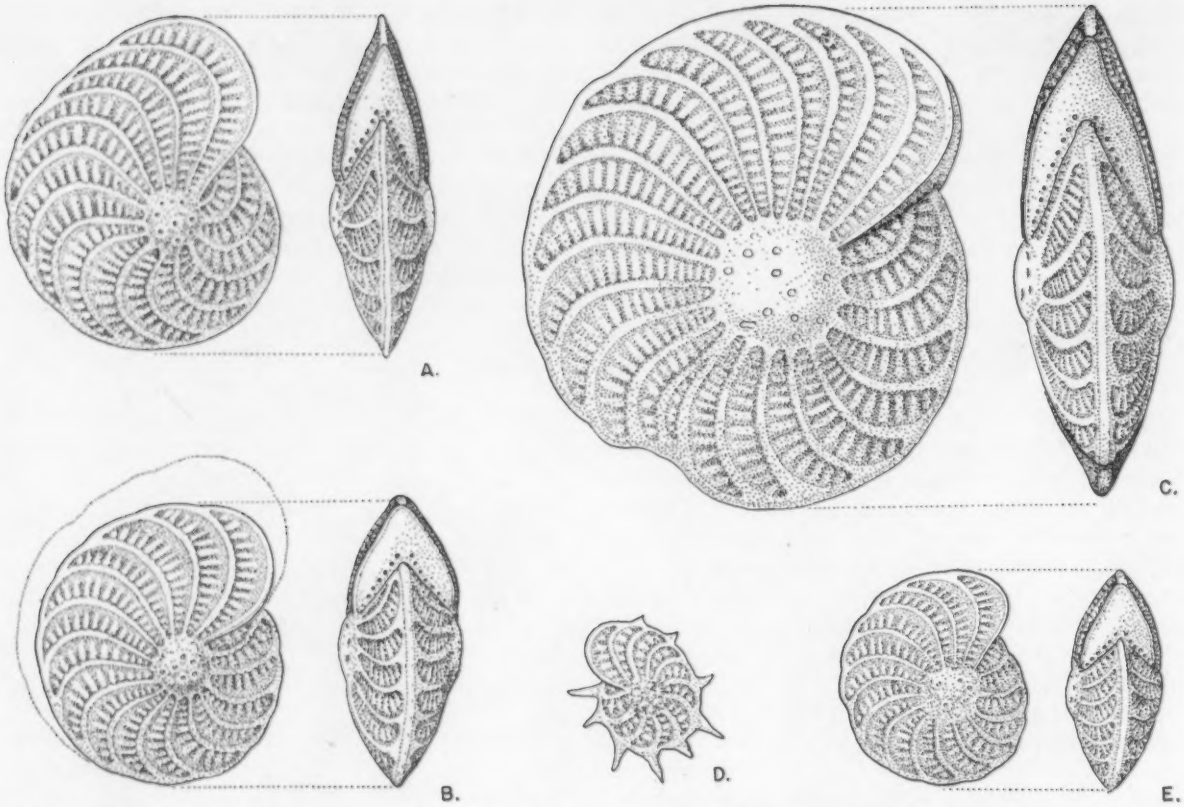


FIG. 4. Tests of *Elphidium crispum*. *A*. Juvenile with long narrow chambers resulting from rapid growth induced by an abundance of food. *B*. Juvenile with shorter, wider chambers and a more circular outline, the result of less favorable feeding conditions. *C*. Mature individual showing an indentation in the margin of the test marking the limit of growth prior to the period of winter dormancy. *D*. Juvenile with spines. *E*. Mature individual from a tide pool where the rate of growth is comparatively slow. *B* would seem to be an intergrade between *A* and *E*, although there is a difference in the texture of the tests from the two zones that cannot be shown in drawings. Based on camera lucida drawings × 625.

species are thicker than those produced in higher latitudes and are often regarded as distinct species. *E. crispum* is universally distributed in coastal waters except for areas within the polar seas, and if slight variations in the shape and texture of the tests which result from the conditions under which they are produced were to be considered adequate to justify the erection of new species and subspecies, the group could be subdivided indefinitely. However, slight differences in test morphology have a decided value to the stratigrapher.

INFLUENCE OF FOOD UPON GROWTH AND REPRODUCTION

In the littoral zone the plankton content of the water that ebbs and flows with each tidal cycle is grazed upon by myriads of animals living at all levels upon the beach; therefore the food of the Foraminifera living in this life zone is limited for the most part to the microflora produced in the substratum upon which they live. The tidal flux also exposes these Foraminifera to abrupt changes in environmental conditions, and their success depends in part upon their ability to make rapid readjustments to a changing environment. In the sublittoral zone, where ecological conditions are more stable, tidal currents and a considerable vertical mixing of the water assure the Foraminifera a maximum amount of food in addition to the microflora living on the bottom, and we have found that these differences in ecological conditions, including the relative abundance of food in the two life zones, are responsible for the fact that in all latitudes populations of Foraminifera living between high- and low-tide level have few species in common with populations living below low-tide level, although as-

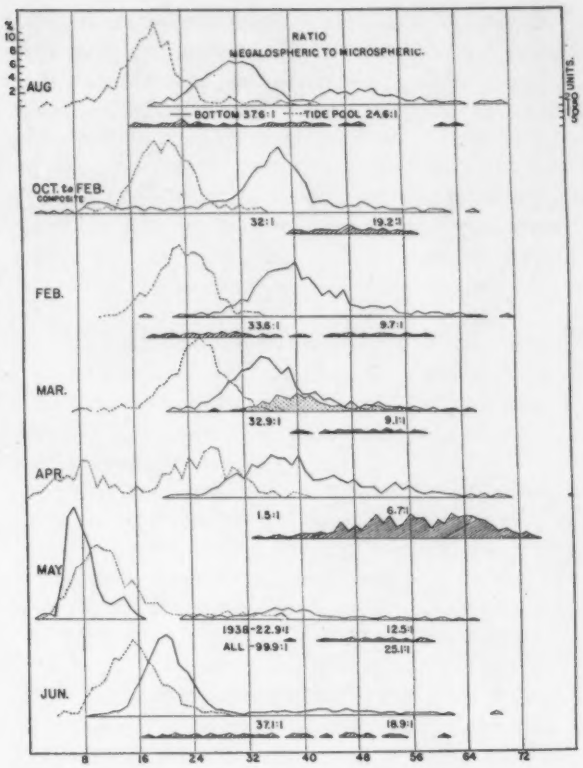


FIG. 5. Percentage frequency-distribution curves for growth stages in *E. crispum* based on the number of chambers in samples of populations. Broken lines represent samples of 500 megalospheric individuals taken in tide pools, and entire lines, 1,000 megalospheric individuals taken in the sublittoral zone. The curves that are cross-hatched are for microspheric individuals in the latter samples, and the stippled area in the curve for March is for megalospheric individuals showing cytological evidence of gametogenesis.

semblages of empty tests of Foraminifera found in sediments taken near the coast include those of species common to both zones. After periods of storm-induced turbulence some mixing of populations takes place, but individuals usually fail to survive for long when removed from their natural habitat to a new environment.

Ecological conditions other than food are probably responsible for the observed distribution of *E. crispum* within Plymouth Sound, and the enormous numbers of individuals in restricted areas within each of the two life zones suggest that this species is well adapted to the conditions within the restricted areas. However, in the sublittoral zone the rate of growth in *E. crispum*, as we have said, is 40 percent greater and the diameter of the test is 60 percent larger than in the littoral zone, and it would seem that this difference in growth is an expression of the relative abundance of food available to these two groups of Foraminifera. This is in agreement with the observed diminution in size of individuals of other species of Foraminifera produced in cultures in which there was a sparsity of suitable food organisms (Myers, 1936).

Winter is a period of dormancy, for both the Foraminifera and the organisms upon which they depend for food, as is evident from the sparsity of food organisms in the distal chambers of the tests and the amount of shrinkage in the protoplasmic content of the earlier-formed chambers (Myers, 1942*a*). After a rapid increase in the numbers of photosynthetic organisms in the plankton in February, thin sections of most species of Foraminifera show enormous numbers of diatoms and other unicellular plants. At about the same time the distal chambers of *E. crispum* contain comparable numbers of the gametes of larger algae, and the protoplasmic content of the earlier-formed chambers shows less and less shrinkage. An increase in metabolic activities results in growth through the addition of new chambers to the test, and after two to four chambers have been added, megalospheric individuals that are at least half-grown produce gametes. Gametogenesis marks the beginning of an intense period of sexual reproduction, which persists for three to four weeks. Near the end of this period vast numbers of juvenile megalospheric individuals are to be found in the sediments, indicating that asexual reproduction by individuals of the larger microspheric generation is taking place. In figure 2 it will be observed that growth, sexual reproduction, and asexual reproduction follow in sequence, and that this period of unusual activity on the part of the Foraminifera coincides with the spring outburst of phytoplankton production. Although the phytoplankton is only one source of food available to the Foraminifera, its relative abundance is probably a dependable index to the productivity of the more important microflora in the substratum upon which benthonic Foraminifera live and take much of their sustenance, because the productivity of both groups of food organisms is largely dependent upon illumination and the nutrient salt content of the water.

INTERPRETATION OF FREQUENCY-DISTRIBUTION CURVES OF GROWTH STAGES

Percentage frequency-distribution curves for growth stages based on the numbers of chambers

in 500 megalospheric individuals in samples of populations taken in tide pools show but a single mode for 11 of the 12 months (fig. 5). Beginning in April, the mode shifts rapidly in the direction of increasing size until August, and then at a diminishing rate until November, when growth is discontinued until the following March. The curve for April has two distinct modes, the first representing a new generation that had been asexually produced by microspheric agamonts, and the second, those larger individuals which had survived from the previous year, and which were about to produce sexual gametes.

A set of curves similar to those discussed above was also prepared for individuals of the microspheric generation in the same populations. From these curves, together with the changing ratios of microspheric to megalospheric individuals, it is evident that sexual reproduction takes place in March, or about one month earlier than asexual reproduction, and there is ample cytological evidence to confirm these dates (Myers, 1942*a*).

When the growth stages in megalospheric individuals in samples taken in the sublittoral zone are plotted in a like manner, the curves for April through September have two distinct modes (fig. 5). From this it is evident that from 10 percent to 22 percent of the population of megalospheric individuals fail to reproduce at the end of the first year and continue to live through the second year. It is also evident that although sexual reproduction takes place at about the same time in both life zones, asexual reproduction occurs in May, or about one month later than in the littoral zone. In the sublittoral zone a second period of asexual reproduction occurs in September, and it is significant that this second period of asexual reproduction also coincides with an intense outburst of phytoplankton production (fig. 2).

No corresponding period of asexual reproduction takes place in the littoral zone, where a shortage of food no doubt results from the feeding activities of an enormously increased population of animal associates compared with that of the previous spring. From these data it is evident that the life span for individuals of each generation is usually one year, and that in the littoral zone only two years are required to complete the life cycle, while in the sublittoral zone reproduction is delayed in a portion of the population until the second year, and three or even four years may be required to complete the life cycle.

Drake's Island.—We know that the shape of the curve representing growth stages in a tide-pool population of *E. crispum* taken on Drake's Island in August was influenced by an intense outburst of phytoplankton in the spring, and that most individuals reproduced within a relatively brief period. This accounts for the few classes of growth stages represented and the abrupt nature of the curve (fig. 6). From a

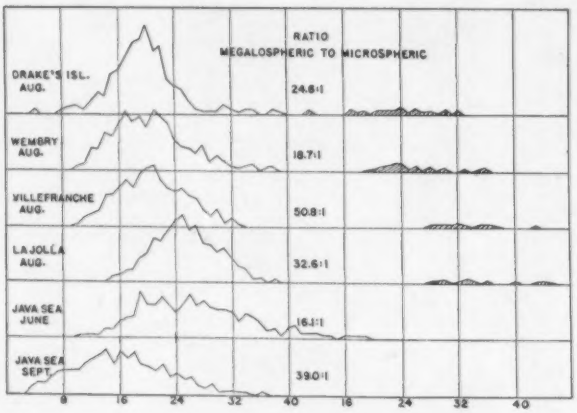


FIG. 6. Percentage frequency-distribution curves for growth stages in *E. crispum* based on the number of chambers in samples of populations numbering at least 500 individuals. The number of classes of growth stages represented suggests the length of the period of reproduction.

series of curves we have determined the maximum number of chambers in tests of this species, the length of the growing season, and the rate of growth (fig. 5). Knowing the time, intensity, and duration of the periods of growth and reproduction in *E. crispum*, we can deduce much concerning the intensity and duration of the major outburst of phytoplankton production from a single frequency-distribution curve of growth stages in a sample of a population taken in a region where little or no data are available concerning the phytoplankton cycle in the sea, as we shall endeavor to explain.

Wembry.—At Wembry, near the entrance to Plymouth Sound (fig. 1), the coralline algae upon which *E. crispum* lives are exposed to heavy surf produced by ground swells from the open channel. In the early spring the scouring action of the water delays the development of a substratum rich in the unicellular plants upon which the Foraminifera graze. A more limited supply of food delays the recovery of the Foraminifera from winter dormancy, reduces the rate of growth, and extends the periods of reproduction.

For these reasons the frequency-distribution curve for a sample taken at Wembry in August is broader, more depressed, and has more secondary modes than the curve discussed for a similar sample taken on the same day on Drake's Island within the more sheltered portion of the sound (fig. 6). Curves for samples taken on coralline algae at Cawsand and Bovisand were similar to those for samples taken at Wembry, because these stations also were exposed to heavy surf action. The mean number of chambers in the two samples represented by curves in figure 6 were 18.2 and 19.8, respectively—a difference of 1.6 chambers. At the usual rate of growth this is the equivalent of a difference of 10 days' to 2 weeks' growing time.

Villefranche.—The mean number of chambers in a sample of a population of *E. crispum* taken near Villefranche on the Mediterranean coast of France in August of the following year was 20.8 (fig. 6). The plankton content of the water in this region is known to be relatively low, and the season is considerably advanced compared with that at Plymouth. At Plymouth the spring of 1939 was more favorable to the Foraminifera and the organisms upon which they depend for food than was the preceding year, and conditions at Villefranche were probably likewise more favorable. Therefore the slight difference in the number of chambers produced suggests that the rate of growth at Villefranche is relatively low in spite of the fact that the tidal range in this region is so slight that the Foraminifera remain submerged at all times and are therefore not subjected to those adverse conditions which develop on a beach exposed at ebb tide.

The depressed nature of the curve for this sample is indicative of a period of reproduction that possibly was less intense than that which had resulted in the curve obtained for the Drake's Island sample.

La Jolla, California.—The curve for a sample taken from a tide pool near La Jolla, California, in August of 1937 (fig. 6) is less abrupt than that for the Drake's Island sample and more abrupt than those for samples from the other stations discussed. This suggests a spring outburst of phytoplankton production somewhat intermediate between those occurring at the other stations. The difference in the mean number of chambers produced before September at La Jolla could have resulted from a difference in the rate of growth of the geographical subspecies found locally, compared with that of the European subspecies, or from a more abundant and persistent supply of food.

The maximum number of chambers in tests of *E. crispum* from a sample taken at La Jolla in November at the end of the growing season was also comparably greater than the numbers obtained at the other stations. This difference in the limit of growth is probably due to a longer growing season and to more intense summer outbursts of phytoplankton production. This production results from the upwelling of water rich in nutrient salts from the intermediate depths—a movement brought about by the drift of surface water away from the coast in this region. This increased supply of plant food supports a luxuriant growth of algae along this coast, as seen in the great beds of the giant kelp, *Macrocystis pyrifera*. For reports of phytoplankton production at La Jolla, see W. E. Allen (1928).

Java Sea.—In the western portion of the Java Sea temperature, salinity, illumination, and other conditions remain relatively constant, and there is no evidence of a change of season on the islands of the region (fig. 7). In a shallow tropical sea nutrient salts are utilized by the microflora almost as soon as they become available, and an impoverished condition of the water as regards plant food and plankton organisms is presumed to persist at all times. Two samples of populations of Foraminifera from reef weed taken on Poelo Kelapa in the Thousand Islands near Sunda Strait show wider variations in growth stages than the conditions would suggest as possible (fig. 6). The relatively smooth depressed curves representing these populations show more classes of growth stages than the curves previously discussed, and when interpreted in the light of earlier observations, they suggest unusually prolonged periods of asexual reproduction and shorter periods of relative dormancy.

The absence of early juvenile stages in June (fig. 6) makes it obvious that no asexual reproduction had taken place for some time. The low ratio of megalospheric to microspheric individuals compared with the ratio obtained in September, and the occurrence of numbers of large megalospheric individuals, make it equally obvious that sexual reproduction was taking place, as was confirmed by the presence of gametes in many of the larger tests. The rate of growth, as determined from a series of samples taken at intervals of one month, was found to be somewhat in excess of that observed at Plymouth during the spring and early summer of 1939. Therefore the period of

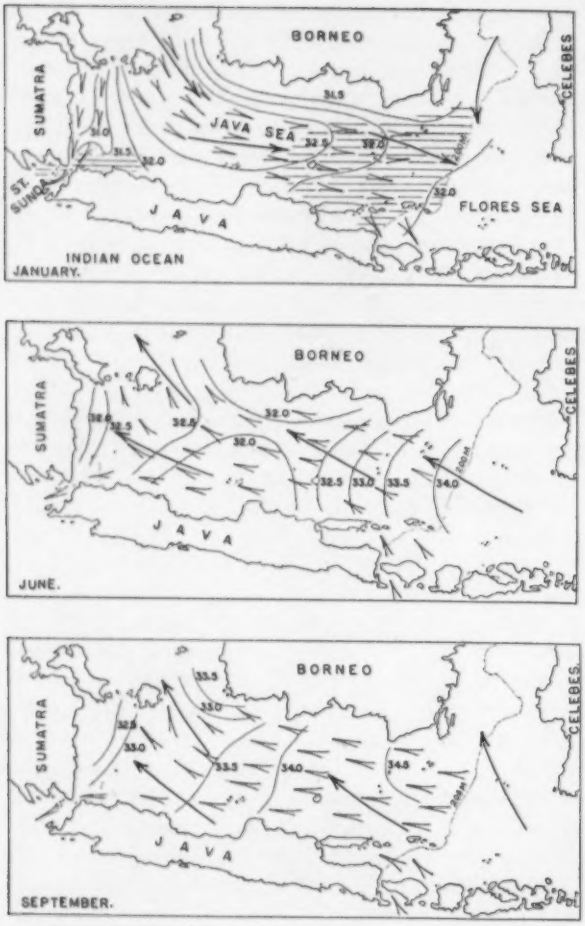


FIG. 7. Probable course of isohalines in the Java Sea. Darts indicate currents, and arrows wind direction. Water temperatures range from 26.5° C. to 28.0° C. with less than 0.5° C. difference between the surface and the bottom. The season of the West Monsoon extends from December to April, during which water from the shallow South China Sea enters the Java Sea, while the season of the East Monsoon lasts from April to December, during which typically oceanic water enters the Java Sea from the Flores Sea and Indian Ocean; thus the water of the Java Sea is exchanged with that of adjacent bodies of water twice each year. Surface water flows outward through Sunda Strait at all times, but there is evidence that a deep current enters the Java Sea through this strait from the Indian Ocean during the season of the West Monsoon at least in occasional years. From seasonal variations in growth stages in the Foraminifera and other evidence it would seem that this was the case in 1940. Shaded areas suggest regions in which species of *Globigerina* are most numerous in the bottom sediments, and where the largest numbers of certain fishes are taken. Conditions in December are similar to those in June except for the direction of the wind and currents.

asexual reproduction that had resulted in this generation of megalospheric gamonts had begun some four or five months earlier, probably in January at the height of the West Monsoon season, which extends from December to March.

Evidence of a second period of asexual reproduction is to be found in the September sample in the number of juveniles that had been recently produced; and from the absence of appreciable numbers of larger individuals it is evident that sexual reproduction had taken place some weeks earlier. This is further suggested by the high ratio of megalospheric to microspheric individuals and by the absence of cytological evidence of gametogenesis. The largest individuals in the June sample were probably produced during the period of reproduction that had preceded the one responsible for the major portion of this population.

From these deductions it would seem that the sequence of events in the life cycle of *E. crispum* is similar in all regions; that is, a period of comparative dormancy is followed by a brief period of growth which in turn is followed by sexual reproduction of megalospheric gamonts and shortly thereafter by asexual reproduction by microspheric agamonts. In the higher latitudes the period of winter dormancy probably results more from a shortage of food than from low temperatures, and in the spring, growth and reproduction are induced by the abundance of food that becomes available at the time of the spring outburst of phytoplankton production. From our experience with cultures we know that after a foraminifer has approached a more or less definite growth limit, a moderate supply of food is sufficient to induce reproduction; therefore it is logical to conclude that in the Java Sea an outburst of phytoplankton production or even a moderate supply of food organisms would induce reproduction in Foraminifera that were approaching the growth limit for the species.

No quantitative studies of phytoplankton production have been made in the Java Sea. Until this is done, it will be impossible to prove or disprove the occurrence of an outburst of phytoplankton production in the region of the Thousand Islands that would explain the occurrence of distinct periods of reproduction in these Protozoa. However, from the data available it would seem that such an outburst is altogether possible, as will be explained. The occurrence of such an outburst of phytoplankton production would also

contribute to a better understanding of the migrations of fishes reported by Hardenberg (1937).

We know that currents induced by the East Monsoon winds pass through the narrow channels between the Thousand Islands from April to December, and that this water, coming as it does from the shallow basin of the Java Sea, is impoverished in nutrient salts. Toward the end of the season, reproduction by the microflora probably approaches a minimum, and a shortage of food would reduce the activities of the Foraminifera to a state verging on dormancy.

Surface water is thought to flow outwards through Sunda Strait at all times, but from salinity determinations (Berlage, 1927) it is evident that in at least occasional years a deep stream of water from the Indian Ocean passes through the strait into the region of the Thousand Islands from December to April. From our observations on the distribution of the tests of pelagic Foraminifera in the sediments (Myers, 1942*b*), it is evident that this water continues along the north coast of Java as far as the Bay of Batavia, which also approximates the limit of the range of the fishes referred to, which enter this portion of the Java Sea only during the season of the West Monsoons. The deeper water of the Indian Ocean is richer in nutrient salts and mixes with the water of the Java Sea in the vicinity of the Thousand Islands. The enrichment of the water in this region would no doubt result in an outburst of phytoplankton production, and with a sudden increase in the supply of food organisms following a period of sparsity, the more mature Foraminifera reproduce. This is the only way in which we can account for the generation of *E. crispum* produced in January of 1940, which are represented by the June sample. Because this outburst of phytoplankton production developed slowly, the period of reproduction in the Foraminifera was extended, and the number of classes of growth stages increased in comparison with those in samples from other regions. As the individuals produced in January approached the growth limit of the species, only a moderate supply of food would be necessary to induce the period of reproduction that began prior to September. It is therefore unnecessary to presume a second period of intense phytoplankton production to account for the second generation. A difference in the state of maturity of individuals, produced as a result of a retarded phytoplankton outburst in January, would result in a corresponding difference in the time when the progeny reached maturity and in turn reproduced. This explains the similarity in the shape of the curves for the two samples under discussion. From these and related data it is evident that in this portion of the Java Sea the usual life span of *E. crispum* is six months, and the life cycle is completed within one year, or in one-half the time required in the higher latitudes.

Evidence of distinct periods of reproduction in these Protozoa suggests that water rich in nutrient salts entered the Java Sea from the Indian Ocean through Sunda Strait during the West Monsoon season of 1940.

Influence of Ecological Factors on Success of *Elphidium crispum*

The substratum.—E. crispum is most successful when submerged at all times, although it does occur on matted growths of algae at levels on the beach that are exposed for brief intervals on unusually low tides. They are most numerous in tide pools where the coralline algae remain relatively free from masking growths of filamentous algae, and where the scouring action of the surf does not remove these and other Foraminifera that remain free and active in the adult stage. *E. crispum*, with its smooth lens-shaped test and weakly developed pseudopodia, is well adapted to graze upon the microflora living upon the densely growing, semirigid fronds of *Corallina*. It is also found in lesser numbers on larger algae and eelgrass, but is more easily washed from this substratum by currents than a species in which at least the ventral surface of the test is flattened or in which the test becomes attached, as in *Planorbulina* and *Cibicides*.

In the sublittoral zone *E. crispum* is most numerous on a bottom composed of firmly packed sand or of a mixture of coarse sand and shell gravel. Suitable areas are usually overlaid with clear non-estuarian water and are o ten in the backwash of a tidal eddy, where, during much of the summer, shifting masses of larger algae that have broken away from the shore cover the bottom. Water-borne food and the rich microflora living on such a bottom contribute to the production of a maximum population of *E. crispum*.

On a sandy bottom the biconvex test of this species offers little resistance to currents, and the radiating pseudopodia loosely bind together a mass of sand which tends to prevent the foraminifer from being dislodged during periods of moderate turbulence. *E. crispum* is not always

numerous in areas similar to those described, but a reasonable amount of exploration along almost any coast will usually reveal a satisfactory source of material.

In protected bays, or in seas where winds of gale velocity are unusual, as in the Java Sea, mud bottoms often support a population of larger species of this genus, but where the empty tests are relatively uncommon in the sediments, it is well to presume that these had not originated in the immediate vicinity, especially if the depth of the water exceeds that at which photosynthetic organisms thrive.

It is somewhat difficult to understand why Foraminifera with vastly different types of tests should occur in the same population, or why species having a particular type of test should succeed under seemingly unfavorable conditions. However, the nature of the substratum definitely limits the distribution of many species, and one quickly learns where to look for a particular species, especially in coastal areas, although it is not always possible to explain why one area appears more favorable than another. In a later paper we shall discuss more fully the test morphology of the Foraminifera of the Java Sea in relation to the substratum upon which they live (see discussion).

Tides.—At Plymouth the amplitude for spring tides is from −7.3 feet to +8.2 feet, or 15.5 feet, while that for neap tides is from −3.8 feet to +3.8 feet, or 7.6 feet, and the extreme amplitude for the year is 19.1 feet. In this region there are two high and two low tides each day that are nearly equal, and the beach at the three-quarter-tide level, where *E. crispum* is most numerous, is exposed on spring tides for more than 7 hours, twice in each 24-hour period. Therefore tide pools at the three-quarter-tide level contain only surface water of minimum salinity and maximum temperature for many hours each day; further, the water entering these pools usually has been grazed upon by myriads of animals living at either higher or lower levels on the beach, so that, after the tide has receded below the level of the pool, the already impoverished food content of the water is further depleted by the animals living within the pool. The possible influence of food on the growth of *E. crispum* living under these conditions has been discussed; also the fact that this species is unable to survive more than mild dessication and therefore does not thrive on that portion of the beach exposed at low tide.

Since the ratio of microspheric to megalospheric individuals in tide pools is considerably higher than in the sublittoral zone (that is, 1 to 25 compared with 1 to 40 or even 50), it is evident that the sexual phase of the life cycle is more successful in tide pools. This is probably because there are no currents to wash away the gametes that are released after the tide has receded below the level of the pools (figs. 5 and 6). This assures an opportunity for a maximum number of pairs of gametes to unite in fertilization and for the zygotic amoebulae to become attached before the return of the tide and the resulting turbulent surf.

Abrupt changes in ecological conditions within a tide pool as a result of the tidal flux often make necessary rapid readjustments on the part of the inhabitants, particularly in the higher latitudes, as we shall endeavour to show. These ecological conditions, including the impoverished food content of the water, are responsible for the fact that in all latitudes populations of Foraminifera living in the intertidal zone have few species in common with populations living below low-tide level. In the following lists *Elphidium crispum* is the only species common to both life zones that exceeded one percent of the living Foraminifera in the samples studied.

TEN SPECIES OF FORAMINIFERA MOST NUMEROUS IN THE SUBLITTORAL ZONE NORTH OF DRAKE'S ISLAND IN AUGUST

	Percent
Elphidium crispum (Linnaeus)	28.0
Rotalia beccarii (Linnaeus)	22.0
Elphidium striato-punctatum (Fichtel and Moll)	16.2
Verneuilina polystropha Reuss	9.5
Nonion depressula (Walker and Jacob)	8.4
Quinqueloculina lata Terquem	5.3
Textularia conica D'Orbigny	3.8
Bulimina elegans D'Orbigny	1.1
Pyrgo depressa D'Orbigny	.6
Quinqueloculina seminula (Linnaeus)	.4
Total	95.3

EMPTY TESTS OF SPECIES OCCURRING IN THE SAMPLES THAT WERE NOT PRESENT IN THE LOCAL POPULATIONS, COMPARED WITH THE NUMBERS OF LIVING FORAMINIFERA IN THE SAMPLE

	Percent
Cibicides refulgens Montfort	54.2
Planorbulina mediterranensis D'Orbigny	15.1
Discorbis globularis D'Orbigny	12.9

TEN SPECIES OF FORAMINIFERA MOST NUMEROUS IN TIDE POOLS OF THE LITTORAL ZONE IN AUGUST

	Percent
Discorbis globularis D'Orbigny	66.3
Elphidium crispum (Linnaeus)	15.2
Hemidiscus perversus Sidebottom	5.0
Cibicides refulgens Montfort	2.1
Cibicides lobulatus (Walker and Jacob)	1.6
Planorbulina mediterranensis D'Orbigny	1.3
Discorbis rosacea (D'Orbigny)	1.3
Quinqueloculina lamarckiana D'Orbigny	1.0
Quinqueloculina contorta D'Orbigny	.6
Gromia oviformis Dujardin	.6
Total	95.0

Temperature.—*E. crispum* and its geographical subspecies succeed where the mean surface temperatures in the sea for the three summer months range from 7° C., as in sheltered bays in south Greenland and the Falkland Islands, to 30° C. in the Red Sea and the Java Sea (Brady, 1884). In Plymouth Sound the mean water temperature for February is the lowest for the year, with an average for 8 years of 8° C., and August is the warmest month, with an average of 16° C., while the total range for the 12 months is 8° C. August is also the month of maximum temperature fluctuations between the surface and the bottom as well as within a single tidal phase, although neither of these fluctuations at Plymouth exceeds 2° C. On a sunny day the temperature of the surface water in a tide pool may be 3° C. above that in Plymouth Sound, although at the depth at which the Foraminifera are most numerous the temperature difference is usually less than 1° C. Therefore the maximum change in temperature to which Foraminifera in a tide pool would be subjected between two tidal phases would seldom exceed 4° C. However, this is equal to about one-half the mean annual range of temperature in the latitude of Plymouth. Under similar conditions in other regions fluctuations of 10° C. may take place within a matter of minutes on successive days with little or no apparent effect upon the distribution of either the Foraminifera or the algae upon which they live.

Growth through the addition of new chambers to the tests of individuals that had survived the winter was first observed in February, when the mean surface temperature was little more than 8° C. or slightly above the minimum for the year. Both growth and sexual reproduction approached a maximum soon after March 15, when the mean temperature was less than 0.5° C. above the minimum for the year. On the other hand, winter dormancy in these Foraminifera, as determined from the amount of shrinkage in the protoplasm, was well advanced by October 15, when the mean temperature was nearly 14° C., or 6° C. above that of March, when the rate of growth and reproduction was at the maximum for the year. In the littoral zone asexual reproduction was well advanced by April 15, when the mean temperature was 9.5° C., while in the sublittoral zone the same conditions were not reached until May 1, when the deeper and somewhat colder water of this life zone was about the same temperature as that observed in tide pools two weeks earlier. This is the only instance in which there would seem to be a correlation between temperature and the life activities of the species under consideration. However, the second period of asexual reproduction in the sublittoral zone occurred in late September, when the mean surface temperature was 15° C., or only about 1° C. below the maximum for the year, and the difference in temperature between the first and second periods of asexual reproduction in the tide pools was 6.5° C., which is equal to a difference of three-fourths the annual range for temperatures in the sound.

When the temperature in cultures of other species of Foraminifera was reduced, growth and reproduction were discontinued (Myers, 1935). Should someone succeed in culturing *E. crispum*, a state verging on dormancy might be induced by lowering the temperature. Such a laboratory experiment would be interesting, but would have little significance because it would not explain why the temperature in the sea at Plymouth was far lower during the period of greatest growth and reproduction in this species than it was during the first half of the period of winter dormancy. Temperature is no doubt an important factor in that it tends to limit the rate of metabolic activities in an organism, but we are forced to conclude that in the vicinity of Plymouth Sound temperature has little influence upon the life activities of *E. crispum*, although it probably does limit the activities of certain other species.

Salinity tolerance.—The maximum range of salinity within a tidal cycle for organisms living near low-tide level on Drake's Island in Plymouth Sound was 26.6 ‰[1] and 34.9 ‰ at low and high tides, respectively, which is a difference of 8.3 ‰ or a change of 5.8 atmospheres of osmotic pres-

[1] ‰ indicates parts per thousand.

sure in a little more than 10 hours. In March, the month of greatest growth and reproductive activities in *E. crispum*, the salinity range for the complete tidal cycle may be only 25.3 ‰ to 26.4 ‰ at low and high tides, respectively, although surface salinities as low as 19.5 ‰ do occur. This low-salinity surface water may remain in tide pools for as long as 7 hours on a spring low tide (Milne et al., 1938). Therefore it is evident that fluctuations in salinity within Plymouth Sound are not sufficient to be a critical factor in the distribution of *E. crispum*. Otherwise this species would not have occurred at all levels on the beach below the three-quarter-tide level.

A heavy rain may cause from 2 to 4 inches of fresh water to collect at the surface of a pool, but this does not mix appreciably with the denser sea water except where a pool is exposed to strong winds. Consequently this fresh water does not usually extend to the depths at which Foraminifera are most numerous.

The upper limits of salinity tolerance in a balanced aquarium that had been allowed to slowly evaporate was 48 ‰, which is far in excess of salinities observed in the ocean. Therefore a range in salinity from 19.5 ‰ to 48.0 ‰ is well within the salinity tolerance of this species. However, continued low salinity appears to be unfavorable, for *E. crispum* does not thrive in estuaries.

Nutrient salts.—*E. crispum*, in common with most free-living rhizopods, is holozoic. It is thus doubtful whether the dissolved nutrient substances in the sea have an appreciable effect upon its metabolism except in so far as they influence the production of the photosynthetic organisms which constitute the principal source of food for this foraminifer. Periods of growth and reproduction in *E. crispum* more or less coincide with the periods when nitrates, phosphates, and silicates are most abundant. However, they also coincide with the periods when food organisms which utilize these nutrient salts are also most abundant (fig. 2). In the winter, when the nutrient salt content of the water approaches a maximum, the limited amount of illumination reduces the productivity of photosynthetic organisms to a minimum; and with a reduction in the amount of particulate food, the Foraminifera reach an inactive state verging on dormancy. The shape of the test of this species is altered by the rate of growth, but the thickness of the walls seems to bear no relationship to the mineral content of the water or to other chemical and physical conditions in the water at any latitude.

Hydrogen ion or pH.—The hydrogen ion concentration of sea water in equilibrium with the air lies close to pH 8.1. In the sea it may vary from 7.8 to 8.3 owing to the withdrawal of carbon dioxide by plants during photosynthesis. This tends to increase the alkalinity or the pH, while carbon dioxide exhaled by animals or derived from the oxidation of organic matter tends to increase the acidity or decrease the pH. The buffer reaction of certain salts in the sea tends to maintain a state of equilibrium between the hydrogen, bicarbonate, carbonate, and hydroxyl ions, but in a tide pool an unbalanced condition may result from the predominance of plant life over animals. On a sunny day alkalinities as high as 9.5 have been observed (Harvey, 1939), while in estuaries, such as that of the River Tamar entering Plymouth Sound, the amount of carbon dioxide released by the decomposition of organic matter may increase the acidity to 7.5 (Huntsman, 1918).

Small species of Foraminifera survive a pH of 7.0 that develops when excessive amounts of organic matter in an aquarium decompose, although *E. crispum* usually falls from the walls when the pH is depressed below 7.3. Where other ecological conditions are favorable, the pH is rarely a critical factor in the success of benthonic Foraminifera.

Oxygen tension.—An increase in temperature decreases the solubility of oxygen in sea water. Oxygen derived from the atmosphere, supplemented by that released in the synthesis of carbohydrates by the phytoplankton, approximately saturates the surface water in the sea. In tide pools a sunny day often causes the release of more oxygen by the macroflora than the water can dissolve, with the result that the excess oxygen collects in small bubbles on all surfaces. Zoöxanthellae living as inclusions in the cytoplasm of the Foraminifera provide a direct source of oxygen, but these symbiotic algae do not occur at the latitude of Plymouth, and are not essential to the success of most species (plate 1, fig. 5). With an increase in depth, there is usually a decrease in the oxygen content of the water, but in the shallow water of Plymouth Sound and the English Channel, there is sufficient vertical circulation to maintain a high oxygen tension at all seasons (Harvey, 1934). For these reasons oxygen tension is seldom if ever a critical factor.

Illumination.—Most Foraminifera are positively phototropic and negatively geotropic. Prior to reproduction these responses cause the Foraminifera to take up positions on the algae or other objects where the gametes or progeny, when released, are easily dislodged and disseminated by currents. In the late fall this tropistic behavior is evidently reversed, particularly in the microspheric generation, and we find the Foraminifera retreating into crevices between the holdfasts and encrusting fronds of coralline algae or into other protected niches. This reaction probably explains the gradual increase in the proportion of microspheric to megalospheric individuals observed throughout the winter, which could not have resulted from sexual reproduction at this time because there was no cytological evidence of gametogenesis by megalospheric gamonts and no microspheric juveniles were observed (fig. 5 and Myers, 1942*a*). The absence of zoöxanthellae in the Foraminifera at Plymouth may be attributed to the long winters with few hours of sunlight each day.

Turbulence and currents.—Turbulence and current action are the principal forces responsible for the dispersal and geographical distribution of the Foraminifera, although floating algae and other material, as well as wandering or migrating animals that become encrusted with a fauna and flora consisting of algae, barnacles, hydroids, bryozoans, and other organisms, are contributing factors. The gametes of the Foraminifera, as in other animals, are a transition stage that remains viable for only a short time. It is thus probable that the principal method of dispersal is through the juvenile or even adult individuals that are thrown into suspension by turbulence and transported to new areas by currents (Myers, 1936).

When surface sediments are thrown into suspension by wind-induced turbulence, the Foraminifera, because of their lesser density and shape, settle through the water more slowly than quartz sand and come to rest at or near the surface of the heavier sediments. When Foraminifera are buried to a depth not exceeding 5 to 7 times the diameter of the test in sandy sediments, or in the case of the larger *E. crispum* to a depth of about 1 cm., they are able to escape. If buried more deeply, they die within a few months, or even more quickly should the oxygen supply beneath the surface of the sediments be insufficient to sustain life—a condition often made evident by the blue-black sulphides deposited on the walls of the tests or by the presence of iron pyrites within the tests. Should the Foraminifera survive, later periods of turbulence may deposit them sufficiently near the surface so that they regain it and resume normal activities. Most Foraminifera taken between October and March, both in tide pools and in the sublittoral zone, remained inactive when placed in an aquarium, and it is apparent that in the sea they would make little or no attempt to remain at the surface of the sediments during the winter. For this reason it was necessary to examine approximately 500 times more surface sediments in December than in August, to obtain suitable samples of populations of *E. crispum*. From this we may conclude that within the zone of turbulence few Foraminifera remain at the surface of the sediments during the winter, and the rate of survival is suggested by the difference in the numbers of living Foraminifera per unit area before and after the period of frequent and heavy storms. In one area the population in September, as determined from material obtained through the use of a special suction grab (Hunt, 1926) that takes a sample having a definite unit area, was 1,225 per square foot, compared with 245 per square foot in March. From these and other data it would seem that turbulence and current action in the sublittoral zone are responsible for the destruction of at least 80 percent of all individuals that survive beyond the juvenile stage. In tide pools from which most of the larger algae are stripped by the surf after October, a similar proportion of the population is also destroyed by these same agencies (Myers, 1942*a*).

From these observations we may conclude that in some areas turbulence and current action are important factors in the success or failure of a species, and this probably explains the absence of appreciable numbers of *E. crispum* in samples taken in the English Channel.

Turbidity.—Turbidity in the sea limits the depth to which light penetrates, and in turn the depth of the column of water in which photosynthetic organisms are able to utilize nutrient salts. Therefore it limits the production of the food of the Foraminifera both in the phytoplankton and in the microflora living on the bottom as well as the larger algae that provide a habitat essential to the success of many species of Foraminifera. The effect of these conditions upon the distribution of the Foraminifera was studied in our survey of the Java Sea. Certain species that were numerous at depths of 10 to 20 meters in the eastern half of the sea were found at increasing

depths down to 80 meters as the entrance to the Flores Sea was approached (fig. 7). Secchi disc readings at the limits of this range vary from 5 to 12 meters and from 25 to 30 meters, respectively. The depth to which photosynthetic organisms thrive is considered to be about 2½ times the Secchi disc readings.

The River Plym discharges quantities of clay into Plymouth Sound during heavy rains. *E. crispum* living on larger algae survives where this clay remains in suspension for days or even weeks at a time, and where this material is occasionally silted out in such quantities as to cover the algae with a heavy film. However, it would be unusual to find appreciable numbers of Foraminifera living on mud bottoms adjacent to such an area.

From our knowledge of the distribution of benthonic Foraminifera based upon the protoplasmic casts that remain after the sample is treated with acid, and from our knowledge of the food requirements of these Protozoa as determined from cytoplasmic inclusions, it would seem that the depth of the photic zone as influenced by turbidity has a decided effect upon the quantity of food available, the nature of the substratum, and the depth to which many species of Foraminifera are able to succeed.

Animal Associates

The densely growing, semirigid fronds of coralline algae provide a protected habitat for myriads of small animals, including many species of Foraminifera. A 1-cc. sample of the finer washings from a handful of these algae, taken from a tide pool on Drake's Island in July, contained 573 living Foraminifera, including 91 *E. crispum* in addition to 474 animal associates. These animal associates included representatives of most of the phyla of the animal kingdom and consisted of minute species and juvenile stages of larger species. Among the phyla most abundantly represented, there were 204 Mollusca, 118 Annelida, 115 Arthropoda, 16 Bryozoa, and 13 Nematoda.

A sandy bottom in the sublittoral zone supports a smaller population of animal associates because of the smaller numbers of sessile mollusks and the larger size of the majority of the inhabitants. No numerical study of populations of animal associates was made from this area, although the suction grab used for population studies of the Foraminifera was actually devised for this purpose.

Animal associates not only compete with the Foraminifera for space, but many are more or less dependent upon the same food organisms. We have determined that certain of these associates, including annelids, arthropods, and flatworms, consume numbers of smaller Foraminifera and the juvenile stages of larger species; and that, in turn, these associates provide the Foraminifera with a limited amount of food in the form of eggs, less violently active larval stages such as veligers and trochophores, and the residual protoplasm contained in cast exoskeletons and the bodies of dead organisms.

Parasites and Enemies

From 3 to 5 percent of *E. crispum* taken in the sublittoral zone in the early spring contain developmental stages of the protozoan parasite *Trophosphaera planorbulinae* (Calvez), which Calvez (1936) has assigned to the order Coccidiida. This parasite develops in the protoplasm of the larger chambers and may extend throughout the entire test, destroying the host. Nematode worms also invade the tests in the early spring, and although paraffin sections usually show the protoplasm shrunken away from these worms, the presence of eggs and larval stages in the tests suggests that this is actually a case of parasitism and not a mere invasion of the tests by the worms.

The common shrimp, *Crago vulgaris*, is for the most part a bottom-feeding herbivore, but during the winter, when the microflora on the bottom is sparse, the digestive tract of this arthropod often contains, in addition to sand and plant detritus, from 8 to 14 or more entire or broken Foraminifera that were living at the time they were ingested. It is interesting that *C. vulgaris* continued to feed upon the Foraminifera for some weeks after the microflora that is the natural food of this animal had again become abundant. When food is sparse, most animals living in the sea eat whatever nutrient material is available, and animals feeding upon a substratum composed of minute plants and animals ingest Foraminifera living in this substratum either by accident or through choice. This explains the occurrence of Foraminifera in the digestive tract of many invertebrates, including echinoderms, annelids, flatworms, and arthropods. Certain holothurians and astropectins living in the Tropics ingest enormous numbers of Foraminif-

era, and at times these no doubt constitute the principal source of food. The tests of Foraminifera found in the faeces of many invertebrates show no more evidence of erosion than the tests found in the sediments, and it is evident that the tests of most species could pass through the digestive tract of the invertebrates studied many times before they would be appreciably dissolved.

Discussion

No previous attempt to determine the possible influence of ecological conditions in the sea upon the productivity of the Foraminifera has come to our attention. The present work is therefore limited in scope, but the results and conclusions demonstrate that the methods used could, if applied to other species living under various conditions, contribute to a better understanding of problems in stratigraphy and paleoecology where the fossilized tests of Foraminifera are the principal biotic constituent in geological marine sediments.

Many factors contribute to limit the geographical and bathymetric distribution of a species. Temperature or conditions associated with temperature are of primary importance. Depth and salinity have also been stressed as limiting factors, but the Foraminifera are animal organisms and as such depend upon particulate food for sustenance; therefore the nature of the food available to these Protozoa is largely determined by ecological conditions, including the depth of the water.

The Foraminifera are perhaps as diverse in their food requirements as in the way in which they utilize it; that is, the food may be ingested before being digested, as in many of the unattached Milliolidae, or it may be reduced by digestive ferments in the pseudopodia before it is taken into the test, as in species of *Elphidium* and *Calcarina*, where the apertures of the test are minute. Some species depend primarily upon organisms in the plankton, as in the pelagic Globigerinidae, or upon sessile forms, as in the Homotremidae, while others depend upon organisms in the substratum, as in most free-living Rotaliidae and Miliolidae, or they may utilize organisms found both in the substratum and in the plankton, as in species of *Elphidium* and *Amphistegina*. In the Foraminifera, as in other free-living Protozoa, growth and reproduction take place when the supply of food is in excess of the basic requirements of the animal. In *E. crispum* the varying length and width of the chambers suggest interruptions in the rate of growth which result from a shortage of food or other adverse conditions. When the rate of growth, as determined from frequency-distribution curves based on growth stages, is correlated with measurable ecological conditions in the sea, it is possible to evaluate to some extent the relative importance of these conditions as limiting factors in the success of the species. These varying ecological conditions, acting simultaneously upon the several phases of the life cycle, make it somewhat difficult to estimate the possible effect of a particular condition when comparable changes in magnitude are taking place in other conditions. In Plymouth Sound it would seem that conditions which favor the production of an abundant microflora both in the water and on the bottom also favor growth and reproduction in the Foraminifera. Knowledge of the limits of variation in ecological conditions in this area, where the species is most successful, eliminates from serious consideration as limiting factors similar conditions in other regions, unless it can be proved that these conditions are detrimental when reinforced by other conditions. A hypothetical example would be the possible adverse effect of temperatures similar to those observed in the Java Sea (27° C. ± 1° C.) and of a salinity approaching the minimum observed at Plymouth (25 ‰). We know that *E. crispum* succeeds in both regions and that these conditions acting independently are not detrimental, but together they might limit the distribution of the species. Unfortunately data on this and similar problems are not yet available.

The nature of the substratum, particularly where there is a considerable macroflora, and the degree to which the bottom sediments are disturbed by turbulence and currents are also of primary importance. We find that there is often a distinct correlation between test morphology and the nature of the substratum upon which a species lives. *Marginopora*, *Planorbulina*, and similar attached forms are protected from surf and tidal currents because the large discoidal tests are exceedingly thin. The test of *Operculina* is equally large and depressed, but this form is limited to soft mud bottoms. The equally large *Heterostegina* and *Operculinella* have tests in which the umbilical region has considerable thickness, and these species, provided with heavier tests, are restricted to firmer bottoms where the sediments contain much coarse material or are covered with

a scattered macroflora. Species such as *Tinoporus* and *Calcarina*, in which the test is provided with heavy perforated spines, are found on densely growing algae, while *Rotalia pulchella*, with proportionately longer spines, is often the dominant species where the surface sediments are little more than a colloidal suspension. However, it is also true that certain species inhabit bottoms to which they seem poorly adapted. For example, it is difficult to understand why species with massive tests and not unusually long or numerous pseudopodia, such as *Elphidium craticulata* and *Rotalia papillosa*, should inhabit soft mud bottoms. These observations will be more fully discussed in a later paper.

Elphidium crispum or its geographical subspecies are usually numerous in clear, non-estuarian coastal waters where an appreciable macroflora exists on the bottom. Either this or related species are often found on mud bottoms at depths which, in our experience, do not greatly exceed that of the photic zone and where the bottom sediments are not disturbed by wind-induced turbulence or strong tidal currents during the major portion of the year. The present bathymetric distribution of *E. crispum* and the relative abundance of the tests in certain Tertiary formations make this species a useful guide to the probable depth and the proximity to the coast at which the sediments were deposited.

Summary

1. The life activities of the foraminifer *Elphidium crispum* (Linnaeus) were studied from frequency-distribution curves of growth stages, based on the number of chambers in the test of samples of populations taken monthly for 12 months. The observed sequence of events was correlated with measurable ecological conditions in the sea.

2. The major part of the work was based on samples taken in the vicinity of Plymouth, England, where extensive studies have been made on marine ecology. Additional samples from the Mediterranean coast of France, the coast of southern California, and the western portion of the Java Sea are also discussed in relation to conditions prevailing in the respective areas.

3. It was found that in temperate regions the life span is usually one year, and in tide pools the life cycle, including a sexual and an asexual phase, is completed in two years, while below low-tide level three or even four years may be required. In tropical waters the life span is about six months, and the life cycle is completed in one year.

4. Growth and reproduction are limited for the most part to the spring months, when water temperatures are low, and the period of winter dormancy is well advanced before the temperature has fallen appreciably below the summer high.

5. The major source of food consists of unicellular plants living on the bottom and in the water. Therefore growth and reproduction in this protozoan closely parallel the phytoplankton cycle in the sea.

6. Individuals of *E. crispum* living below low-tide level produced 40 percent more chambers and a 60 percent larger test than those living in tide pools, largely as a result of the relative abundance of food. The rate of growth has a decided effect upon test morphology in this species and varies somewhat from year to year.

7. Variations in salinity, temperature, illumination, nutrient salts, turbidity, and other conditions seem to have little influence upon the productivity of the species, as compared with food.

8. Approximately 80 percent of the individuals produced in these two life zones are destroyed in the late fall and winter as a result of turbulence and current action.

9. Populations in excess of 1,000 individuals per square foot were observed. The annual rate of increase over the winter low is about thirty-fold and forty-fold in the littoral and sublittoral zones, respectively, and the rate of mortality is equal to the rate of productivity.

10. Differences in ecological conditions account for the fact that the littoral and sublittoral zones have few species of Foraminifera in common, although the tests of both populations are found in offshore sediments.

11. Knowledge of the influence of food upon the life activities of the Foraminifera in regions where quantitative studies of phytoplankton production have been made, makes it possible to deduce much from similar frequency-distribution curves of growth stages in populations from regions where no studies of the food content of the water have been made, as in the Java Sea.

12. Animal associates, parasites, and enemies are discussed, as well as the influence of test morphology upon the feeding habits and the distribution of other species.

Acknowledgments

In a series of papers extending over the past 12 years investigators have stressed the need for further work in the field of marine ecology in relation to the Foraminifera, and have explained the value of this work in stratigraphy and paleoecology. Recognition of this need is responsible in part for the recent erection of a subcommittee of the National Research Council to deal with these problems. The present paper is the second of a series designed to extend our knowledge of the significance of the tests of Foraminifera found in recent and geological marine sediments. The field work was made possible through grants from the Guggenheim Memorial Foundation and the Treub Laboratories of the Netherlands East Indies, and is being continued on a Penrose Grant from the Geological Society of America at the Woods Hole Oceanographic Institution. The major portion of the field and technical work was done at the Laboratory of the Marine Biological Association at Plymouth, England, where extensive studies have been made on chemical and physical conditions in the sea in relation to plankton production. My wife Ethel is responsible for much of the technical work and assisted with the manuscript.

Note.—Since this paper was submitted for publication, Dr. Margret W. Jepps has published an account of her studies on *Elphidium crispum* made at Plymouth, England, in 1938–39, the same year that the major portion of the material for the present paper was collected. The two papers have little in common other than the further substantiation of the basic facts of the life cycle established by Lister (1895), who also worked at Plymouth. Neither of these recent studies has advanced materially our knowledge of the origin and fate of the nuclei in the several phases of the life cycle, but it is to be hoped that through the establishment of the time and duration of the periods of reproduction it will be possible to solve this fundamental problem, for through its solution the chromidial theory of Hertwig as applied to the Foraminifera will no longer be tenable.

Literature Cited

Allee, W. C. 1923. Studies in marine ecology. I. The distribution of common littoral invertebrates of the Woods Hole region. *Biol. Bull.* **44**: 167–191.

Allen, Winfred Emory. 1928. Review of five years of studies on phytoplankton at southern California piers, 1920–1924 inclusive. *Bull. Scripps Inst. Oceanography, Tech. Ser.* **1** (16).

Berlage, H. P. 1927. Monsoon currents in the Java Sea. *Koninklijk Magnetisch en Meteorologisch Observatorium te Batavia.* (A Report.)

Brady, H. B. 1884. Report on the Foraminifera dredged by H.M.S. Challenger, during the years 1873–1876. *Challenger Reports* **9**, Zoology.

Calvez, Jean le. 1938*a*. Recherches sur les foraminiferes. *Protistologica*—86. *Arch. zoöl. expér. et gen.* **80**: 163–333.

—— 1938*b*. *Trophosphaera planorbulinae* n. gen. n. sp. protiste parasite du foraminifere, *Planorbulina mediterraneansis*. *Protistologica*—86. *Arch. zoöl. expér. et gén.* **80** (7): 425–443.

Føyn, Bjørn. 1936. Foraminiferenstudien. I. Der Lebenszyklus von *Discorbina vilardeboana* d'Orbigny. *Bergens Mus. Årbok, Naturvid.* 2: 1–23.

—— 1936. Ueber die Kernverhaltnisse der Foraminifere *Myxothaeca arneliga* Schaudinn. *Arch. f. Protistenk.* **87** (2): 272–295.

Hardenberg, J. D. F. 1937. Preliminary report on the migration of fish in the Java Sea. *Treubia* **16** (2): 295–300.

Harvey, H. W. 1934. Annual variation of planktonic vegetation, 1933. *Jour. Marine Biol. Assoc.* **19**: 775–792.

—— 1939. Biological oceanography. In: Symposium on recent marine sediments, Am. Assoc. Petroleum Geologists: 142–152. Tulsa, Oklahoma.

Harvey, H. W., L. H. N. Cooper, Marie V. Lebour and F. S. Russell. 1935. Plankton production and its control. *Jour. Marine Biol. Assoc.* **20**: 407–441.

Hunt, O. D. 1926. A new method for quantitative sampling of the sea-bottom. *Jour. Marine Biol. Assoc.* **14**: 529–534.

Huntsman, A. G. 1918. Vertical distribution of some intertidal animals. *Trans. Royal Soc. Canada*, sec. 4, ser. 3, **12**: 53.

Jepps, Margret W. 1926. Contribution to the study of *Gromia oviformis* Dujardin. *Quart. Jour. Micr. Sci.* **70** (4): 701–719.

—— 1942. Studies on *Polystomella* Lamarck (Foraminifera). *Jour. Marine Biol. Assoc.* **25**: 607–666, 2 pl.

Ladd, H. S., and others. 1941. Report of the subcommittee on marine ecology. *Nat. Research Council Div. Geology and Geography, Ann. Rept.*, appendix A-1.

Lister, Joseph Jackson. 1895. Contribution to the life history of the Foraminifera. *Philos. Trans. Royal Soc.*, ser. B, **186**: 401–453.

Milne, A. 1938. Ecology of the Tamar Estuary. III. Salinity and temperature conditions in the lower estuary. *Jour. Marine Biol. Assoc.* **22**: 529–542.

Moore, Hilary B. 1938. The biology of *Purpura lapillus*. II. Growth. III. Life history and relation to environmental factors. *Jour. Marine Biol. Assoc.*, n. s., **23**: 57–66, 67–74.

Myers, E. H. 1935. The life cycle of *Patellina corrugata* Williamson, a foraminifer. *Bull. Scripps Inst. Oceanography, Tech. Ser.* **3** (15): 355–391.

—— 1936. The life cycle of *Spirillina vivipara* Ehrenberg with notes on morphogenesis, systematics and distribution of the Foraminifera. *Jour. Royal Micr. Soc.* **56**: 120–146.

—— 1940. Observations on the origin and fate of flagellated gametes in multiple tests of *Discorbis* (Foraminifera). *Jour. Marine Biol. Assoc.* **24**: 201–226.

—— 1942*a*. A quantitative study of the productivity of the Foraminifera in the sea. *Proc. Am. Philos. Soc.* **85** (4): 325–341.

—— 1942*b*. Biological evidence as to the rate at which tests of Foraminifera are contributed to the sediments. *Jour. Paleontology* **16**: 397–398.

VAUGHAN, T. WAYLAND. 1940. Ecology of modern marine organisms with reference to paleogeography. *Bull. Geol. Soc. America* **51**: 452–458.

PLATE I

FOOD OF THE FORAMINIFERA

FIG. 1. Paraffin section of a 56-chambered megalospheric *Elphidium crispum* showing the arrangement of the chambers and the position of the single nucleus.

FIG. 2. Section through a *Quinqueloculina* taken in a tide pool that had fed upon fragments of larger algae, filamentous algae, diatoms, and other unicellular plants.

FIG. 3. Section of a *Discorbis* reared in a culture that had fed upon vast numbers of diatoms. The earlier formed chambers and the nucleus show in the upper half of the figure.

FIG. 4. Nucleus of a megalospheric *E. crispum* at a higher magnification than figure 1.

FIG. 5. Section through several chambers of a *Peneroplis* taken on a dead coral reef in which the zoöxanthellae and food organisms probably exceeded in volume the amount of protoplasm belonging to the foraminifer.

FIG. 6. Dividing nuclei, and diatom frustules contained in the cytoplasm of a *Patellina* produced in a culture.

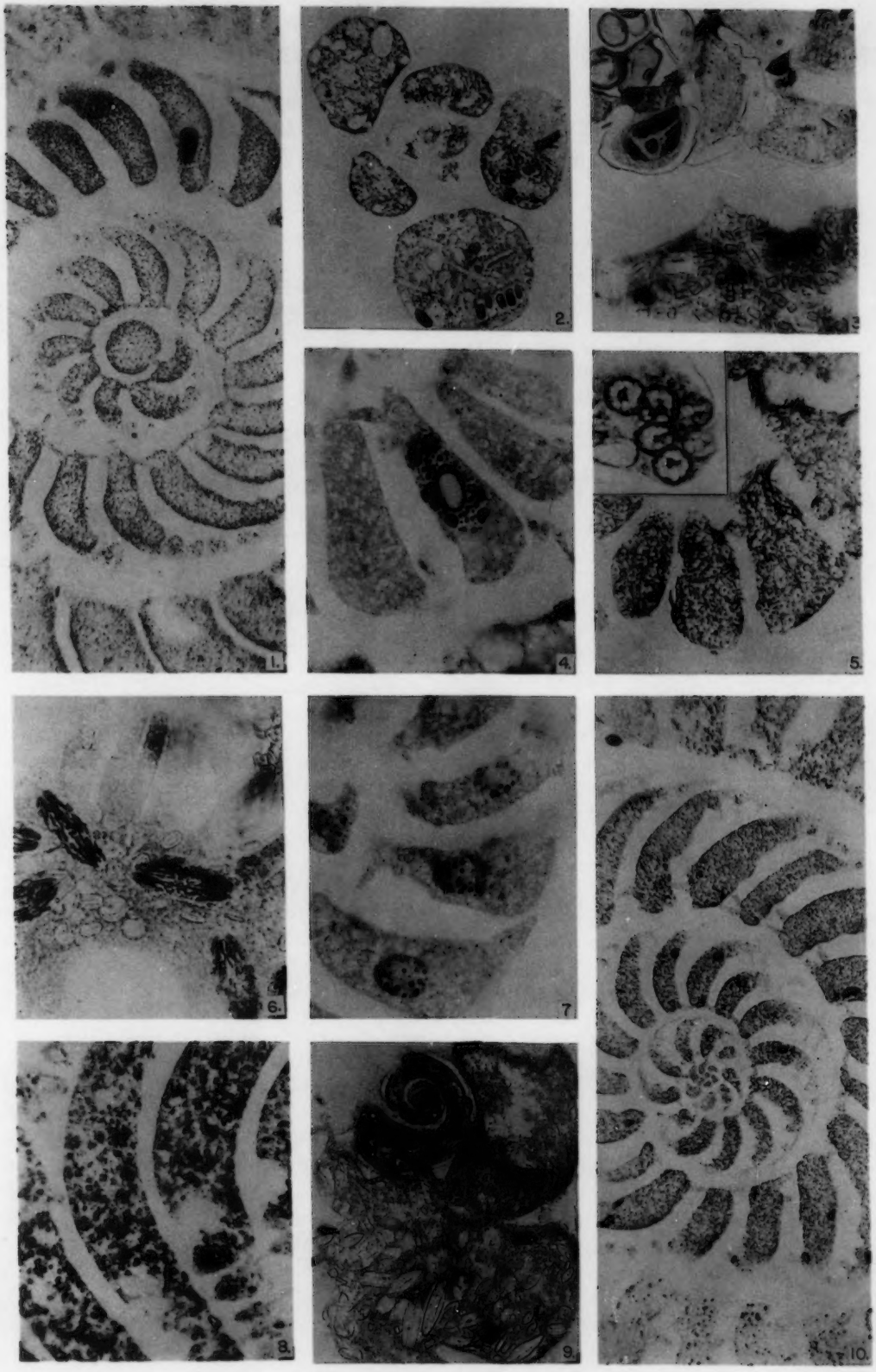
FIG. 7. Several nuclei of a microspheric *E. crispum* at the same magnification as figure 4.

FIG. 8. Partially digested flagellated organisms, presumably the gametes of larger algae contained in the distal chambers of *E. crispum* taken with a dredge. Similar material is contained in the sections of the larger chambers shown in figure 10.

FIG. 9. Section of *Articulina* taken on reef weed showing vast numbers of diatom frustules. The large nucleus is contained in another section.

FIG. 10. Section through a 64-chambered *E. crispum* showing many nuclei and the arrangement of the chambers. Compare with figure 1.

PLATE I



(For description, see opposite page.)

THE EFFECT OF HYDROSTATIC PRESSURE UPON THE EARLY DEVELOPMENT OF THE FROG'S EGG (*RANA PIPIENS*)

I. MACROSCOPIC OBSERVATIONS

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Introduction

In the normal development of the egg, cytoplasmic and nuclear divisions are synchronized processes resulting in progressively smaller cells, each of which receives its appropriate complement of nuclear material. There are various ways in which one can interfere with this sequence of events. Perhaps the most recently utilized method is the application of high hydrostatic pressure (Marsland, 1938). The purpose of this paper is to analyze the effects on development of hydrostatic pressure applied at specific intervals between the time of insemination and the completion of the third cleavage of the frog's egg.

The amphibian egg is one of the most suitable materials for such experimental purposes (Rugh, 1941). This egg was first subjected to variable pressure in 1884 by Pfluger, who found that when he compressed the egg between glass plates before cleavage he could alter the direction of the first cleavage so that it occurred at right angles to the plane of compression. After release of this pressure the eggs developed into normal tadpoles. Since then Hertwig (1893) and Born (1894) repeated Pfluger's experiments with substantially similar results, and Roux (1885 and 1895), who achieved a variable pressure by sucking eggs into glass tubes with diameters less than that of the eggs, was able to alter the cleavage planes from the normal. Similar pressure investigations were carried out on invertebrate eggs by Driesch (1893), Morgan (1893), Ziegler (1894), Wilson (1896), Morgan (1910), Yatsu (1910), Dederer (1910), and Conklin (1912). The last author was able to alter the origin of the micromere in the *Crepidula* egg under pressure. The major contribution of all of these works was that pressure, when its impingement upon the egg is not equal in all directions, alters the cleavage plane only when it alters the maximum axis of the protoplasmic mass with reference to the spindle axis.

Hydrostatic pressure differs from the pressure used in the foregoing studies, since it is transmitted through the liquid medium equally in all directions and consequently does not alter in any way the shape of the egg. Such studies on embryonic development extend back to Regnard (1885), who subjected fish eggs (Salmonidae) to hydrostatic pressures ranging from 1,000 to 10,000 lb. per square inch during the 6-hour period following insemination. Regnard reported punctual and normal hatchings for pressures of 3,000 lb. and lower; delayed but normal hatching at 4,500 lb.; and death before hatching for pressures of 6,000 lb. and more. Draper and Edwards (1932) reported a 15-minute delay for the onset of cleavage, and a high incidence of abnormalities, when the eggs of *Fundulus* were subjected to pressures of 1,000 to 1,950 lb. per square inch.

Quite recently efforts have been made to analyze the action of pressure in terms of the physico-chemical factors which determine the specific phases of development. Marsland, for instance, found (1938 and 1939) that pressure of the magnitude of 6,000 lb. per square inch completely blocked the formation of the cleavage furrows in the eggs of the sea urchin, *Arbacia*. At lower pressures the blocking was only partially effective, and the block was found to be in proportion to the pressure-induced solation of the gelated cortical protoplasm (plasmagel) of the egg. This layer is most conspicuous in the furrow region during active cleavage. It forms an equatorial band which appears to contract and constrict the egg into the blastomeres. Pease and Marsland (1939) demonstrated that the cleavage of a wide variety of eggs could be blocked by equivalent pressures. Also it was shown that pressure differentially conditions several of the other developmental processes: such as the entrance of sperm (Pease, 1942); the elevation of the fertilization membrane (Pease, 1942); the approach of the pronuclei (Marsland,

[1] Aided by a grant from the Penrose Fund of the American Philosophical Society.

1938, and Pease [2]); the formation of spindles and asters (Pease, 1941); and the segregation of daughter nuclei into blastomeres (Marsland, 1939, and Pease, 1941). Most investigators now agree that these diverse effects are, in the main, closely related to the known action of pressure upon the sol-gel equilibria of the various specific parts of the plasmagel system of the egg. (See discussions by Pease, 1941, Lewis, 1942, and Marsland, 1942.)

The aim of the present series of investigations is to determine the effects on the normal sequence of developmental events when hydrostatic pressure is applied in a series of periods during the time between insemination and the third cleavage of the frog's egg. The analysis ultimately will include the effects of pressure upon polar body formation; movements of the pronuclei; syngamy; division and segregation of chromosomes and nuclei; and the division of the cytoplasm. The frog's egg is exceptionally favorable for such a study, since it is readily available throughout most of the year; its time of fertilization can be controlled accurately (Rugh, 1941); the second maturation division is not completed until after insemination, and hence it is possible to include this process in the study; and the stages of normal development under controlled conditions have been timed and plotted with exceptional accuracy.

Materials and Method

The period between insemination and the completion of the second cleavage was divided into ten 20-minute intervals; 3 minutes of each interval being consumed in transferring the eggs to and from the pressure bomb. In each experiment the 10 batches of eggs from a single female were successively subjected to a pressure of 6,000 lb. per square inch, which was maintained until the end of the 20-minute interval. Owing to the transfer time of 3 minutes, the eggs were actually under pressure for 17 minutes. This schedule was designed to demonstrate any differential action of pressure upon successive early developmental processes.

A uniform pressure of 6,000 lb. per square inch was chosen because previous experiments by Pease and Marsland (1939) demonstrated that this was just sufficient to suppress cleavage in the majority of different eggs. The apparatus used in applying the hydrostatic pressure included a large bomb of 250-cc. capacity. In a few instances a microscopic-pressure bomb (Marsland and Brown, 1936) was used. This made it possible to make direct observation of the single egg while under pressure. The magnification was 60 diameters, and a good profile view of the cleavage furrow was allowed.

A total of some 2,000 eggs were studied under various conditions. These eggs were divided into lots of about 100; placed in homeopathic vials of 50-cc. capacity; covered with spring water to a depth of about 7 cm.; and then the vial was filled to overflowing with paraffin oil and placed in the bomb which was also filled with the oil. Control experiments had demonstrated that eggs and sperm maintained under these conditions, but without pressure, were in no way affected (see also Marsland and Rugh, 1940). It required about 3 seconds to build up the pressure to 6,000 lb. per square inch, where it was maintained without any difficulty, and the subsequent decompression was practically instantaneous.

After decompression an immediate analysis of macroscopic conditions was made. Then about half of the eggs of each batch were washed thoroughly in fresh spring water, separated into small groups (to avoid crowding effects), and allowed to develop in finger bowls at 17°–19° C. under the best of conditions. These eggs were observed frequently, in comparison with their control batches, and in some instances a photographic series of the changes was taken.

The other half of each batch of eggs (and a parallel control batch) were fixed in Smith's fluid immediately after compression. This fixed material is now being prepared for cytological studies. These data are to be reported subsequently, and will help to complete the results reported here.

Observations and Experimental Data

Differential Pressure Susceptibility during Early Development

The data of a typical experiment, involving all of the eggs from a single female, are summarized in table 1 and in figure 1. Despite the fact that the duration and magnitude of the pressure treatment was the same in each period, there were marked differences in the effect as measured by the ability of the embryos to survive such complicated developmental processes as gastrulation and hatching. The intervals in which the applied pressure caused the greatest degree of

[2] Personal communication.

TABLE 1

Period of Compression—Min. after Fertilization	Condition of Eggs at Time of Compression	Subsequent Condition of Compressed Eggs at 2 Hr. 50 Min. after Fertilization	Condition of Compressed Eggs 4 Hr. 17 Min.* after Fertilization	Condition of Compressed Eggs at 7 Hr. 2 Min. after Fertilization	Condition of Compressed Eggs at 19 Hr. 22 Min. after Fertilization	Condition of Compressed Eggs at 43 Hr. after Fertilization	Condition of Compressed Eggs at 8 Days after Fertilization
(Min.) 2–19	sperm penetration & migration	0 % cleaving (151 min.)	90 % in 2 cell 10 % in 4 cell (242 min.)	10 % blastulae; younger than controls (6 hrs. 43 min.)	4 % blastulae 96 % cytolyzed	4 % tail bud 96 % died	2 % hatched
24–40	polar body formation, nuclei approach	0 % cleaving (131 min.)	all attempt cleavage, none normal (217 min.)	25 % blastulae; many abnormal cleavages (6 hrs. 22 min.)	20 % attempt to gastrulate; many cytolyzing	all cytolyzed	0 % hatched
43–60	syngamy	superficial attempts at cleavage (110 min.)	1, 2, 4-cell stages, largely irregular (197 min.)	85 % appear normal; some irregular cleavages (6 hrs. 2 min.)	50 % gastrulating 50 % cytolyzed	4 % tail bud 65 % cytolyzed others irregular	16 % hatched
63–80	migration of zygotic nucleus	50 % normal, balance good attempts at cleavage (90 min.)	90 % in 4-cell stage; few slightly irregular (177 min.)	90 % blastulae, normal; 10 % irregular cleavage (5 hrs. 42 min.)	90 % like controls	70 % neurulating 30 % cytolyzing	44 % hatched
83–100	organization for cleavage	About 50 % normal, balance slightly irregular (70 min.)	90 % in 4-cell stage (157 min.)	90 % blastulae, largely irregular; slight delay (5 hrs. 22 min.)	75 % gastrulating 25 % cytolyzed	42 % ahead of controls; balance cytolyzing	30 % hatched
103–120	initial mitotic movements	About 50 % normal; balance abnormal. (50 min.)	90 % in 3–5 cell stages; (137 min.)	90 % blastulae, slight delay and irregular (5 hrs. 2 min.)	50 % gastrulae 50 % cytolyzed	3 % ahead of controls 35 % slightly abnormal 55 % cytolyzed	17 % hatched
123–140	further mitotic movements	No attempts at cleavage; recessions (30 min.)	80 % in 2–5 cell stages, majority irregular (117 min.)	70 % normal, balance delayed & abnormal cleavages (4 hrs. 42 min.)	50 % late blastulae; 50 % cytolyzed	5 % delayed tailbud 95 % cytolyzed	2 % hatched
143–160	anaphase movements; initiation of furrow	No attempts at cleavage; recessions; pressure recently applied (10 min.)	25 % in 4-cell stage 75 % in 0 to multiple cleavages; irregular (97 min.)	50 %–70 % quite normal; slight delay and irregular (4 hrs. 22 min.)	40 % late blastulae	100 % cytolysis	0 % hatched
163–180	cleavage furrow	cleavage; pressure applied here	0–2 cell stages; irregular (77 min.)	Very few normals; irregular cell size; much cytolysis (4 hrs. 2 min.)	30 % delayed but quite normal development	100 % cytolysis	0 % hatched
183–200	mitotic movements toward 2nd cleavage	(pressure not applied as yet)	0–2 cell stages, very irregular	50 % appear normal; 50 % irregular cleavages (3 hrs. 42 min.)	30 % delayed development	100 % cytolysis	0 % hatched
Condition of Control Eggs at Equivalent Times		all in 2-cell stage at 2 hr. 50 min.	90 % in 4-cell stage 10 % in 2-cell stage 4 hrs. 17 min.	All in 32–64 cell stages or early blastulae, at 7 hrs. and 2 min.	Early gastrula, crescent slit.	Early tail bud	All hatched

* In parentheses is given the time after pressure was applied, while at top of column is time from insemination.

derangement in development were during polar body formation, the approach of the pronuclei, and just prior to and during the cleavage process itself. Reciprocally, the period of greatest resistance of the eggs to this pressure was from 63–80 minutes after insemination, *i. e.* in the period after the completion of syngamy but prior to the initiation of the mitotic movements which accompany the first cleavage.

Gastrulation, hatching, and metamorphosis may be considered as the most critical periods in the normal development of the amphibian embryo, and, as the data show, survival of one of these does not guarantee survival through a subsequent crisis. Further, it must not be assumed that the 44 percent that did hatch (from the most resistant pressure interval) were normal, but simply that they were sufficiently viable to achieve the hatching stage and to emerge from their jelly capsules. In fact, these embryos were observed for several weeks, and all of those which approached normal appearance displayed at least some of the characteristics of haploidy associated with parthenogenetic or androgenetic tadpoles

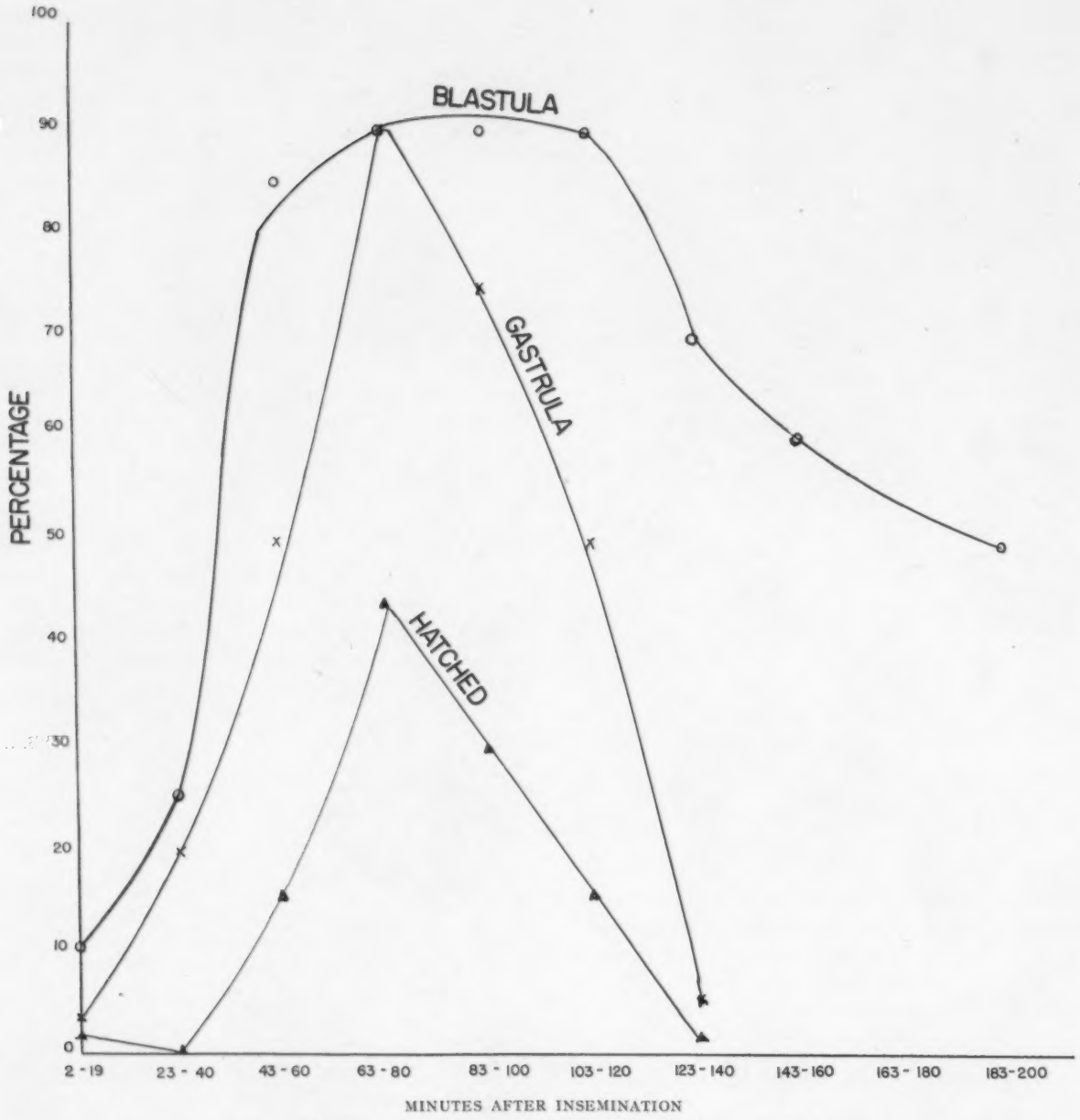


FIG. 1. Pressure intervals after fertilization; 6,000 lb. per square inch.

(Rugh, 1941). This may be seen in plate I, figure 1, which shows a group of these tadpoles at an age of two weeks, with but a single control tadpole at the left.

The Immediate Effects of Pressure upon Furrowing

In the microscopic-pressure bomb it was possible to orient a single egg so that its furrow was seen in profile, and then to apply the pressure of 6,000 lb. per square inch. In contrast with the findings of Pease and Marsland (1939) that a wide variety of eggs show a recession of the furrow while under pressure, the frog's egg responded to hydrostatic pressure by an immediate deepening of the furrow. This is indicated in the series of drawings in figure 2. The application of pressure when the furrow just started to form regularly caused an immediate deepening of the furrow, and a marked recession of the furrow always followed the release of the pressure. The

PLATE I

FIG. 1. Abnormal development of tadpoles after compression. Control tadpole at the left.

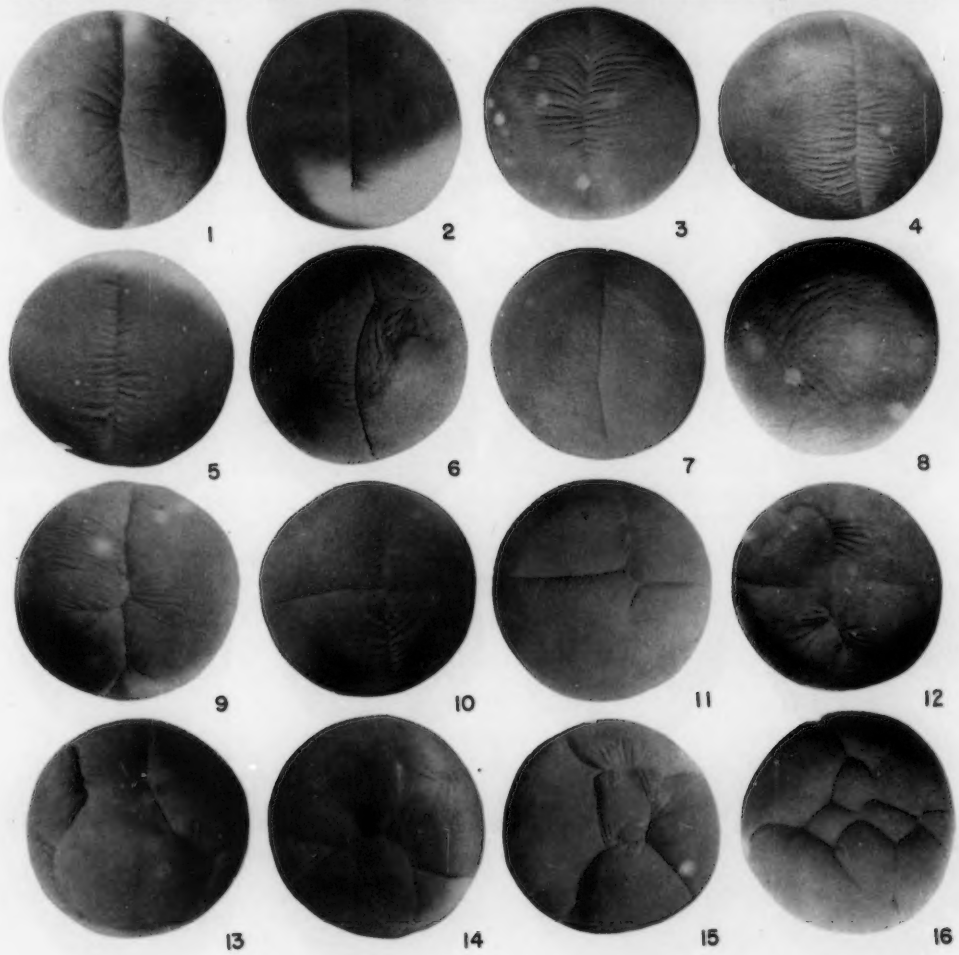
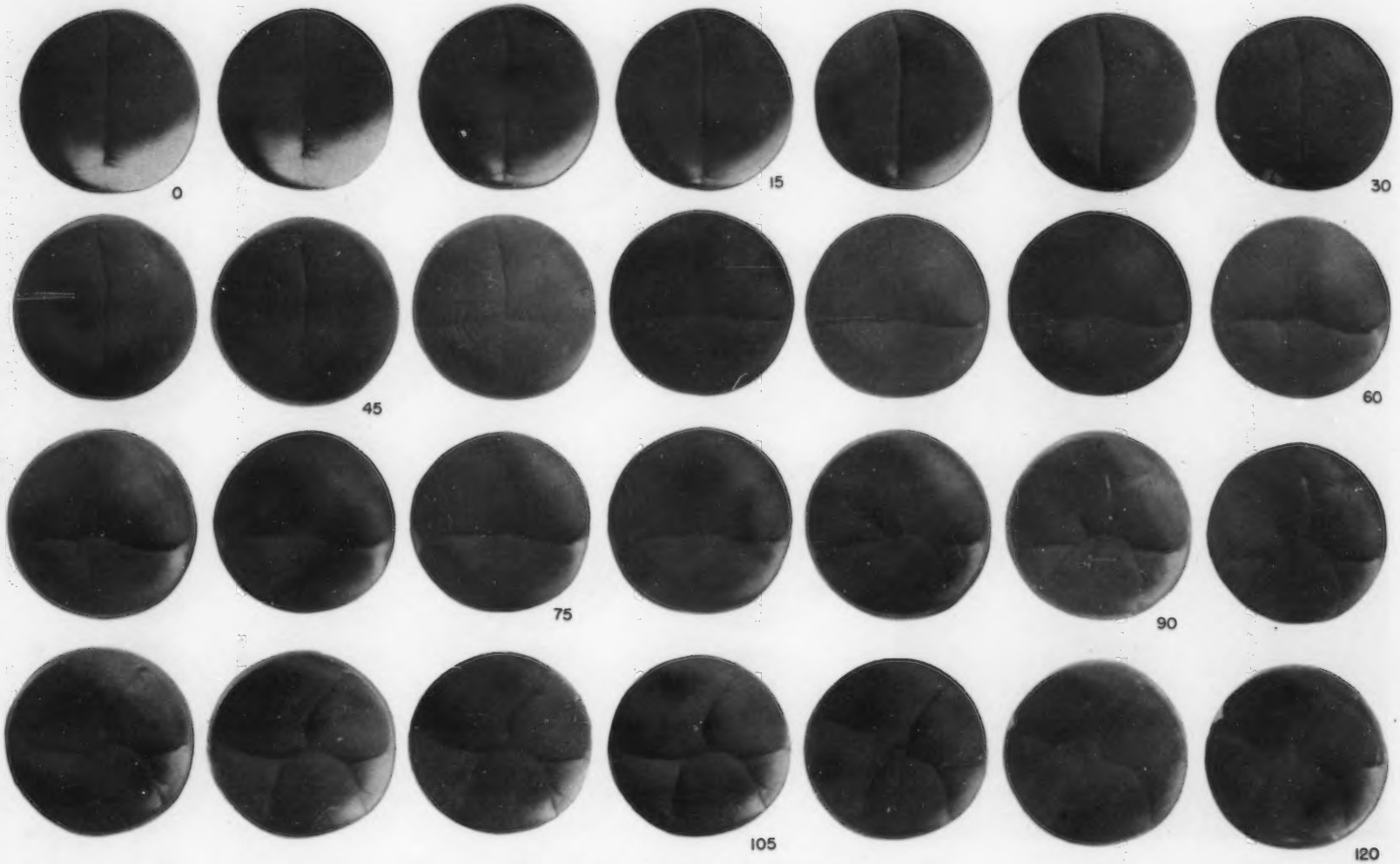


FIG. 2. Abnormal cleavages after compression.

PLATE II



Changes in a single egg after compression.

deepening of the furrows was greater for greater pressures, but the recession was generally complete, if sufficient time was allowed. After several alternate compressions and decompressions, the egg finally failed to respond to the original degree. These pressure effects may be considered as a puzzling anomaly. All other eggs which have been studied have given quite the opposite responses.

Post-pressure Phenomena

All eggs that were cleaving when subjected to pressure, showed deepened cleavage furrows when examined immediately following decompression. However, these clean and deep furrows invariably receded within a short time, although, in some instances, the second furrow began to appear before the recession of the first was complete. Thus it was frequently observed at the time of the four-cell stage of the controls, that the experimental eggs might be in the two-cell stage because of the recession of the first furrow. The appearance of the third cleavage furrow was generally synchronous with that of the controls, but this cleavage was frequently irregular, resulting in eggs with distinct blastomeres numbering 4 or 5 rather than 8, or with many incompletely divided blastomeres, a condition which involved a great deal of superficial wrinkling.

In order to determine the exact sequence of events following the application of pressure on a cleaving egg, a series of 28 photographs of a single egg was taken over a period of 3 hours. The egg did not change position during the series, and it can readily be seen that the furrow was fairly deep when the egg was first removed from the pressure chamber (plate II). Gradually, however, the furrow receded so that by 30 minutes it was a mere superficial crease, and after 60 minutes it had practically disappeared. The second furrow began to appear by this time, at right angles to the original position of the first (receded) furrow. The third furrow began to appear quite normally about 90 minutes after the pressure period. This third furrow made its appearance almost simultaneously with the third furrow of the control eggs, 4 hours after insemination, but the total number of distinct blastomeres in the experimental egg was 4 or 5 rather than the 8 of the controls. This series indicates, then, a partial suppression of at least one of the cleavages, and quite obviously some of the cleavages that did occur were somewhat irregular.

Plate I, figure 2, demonstrates a variety of post-pressure specimens selected to illustrate several other phenomena. Note particularly the converging tension lines of the normal cleavage process (no. 1). These lines are not to be confused with the recession lines (nos. 3–5), which are more generally at right angles to the furrow. The convergence of the normal tension lines might indicate a greater tension, or a maximum

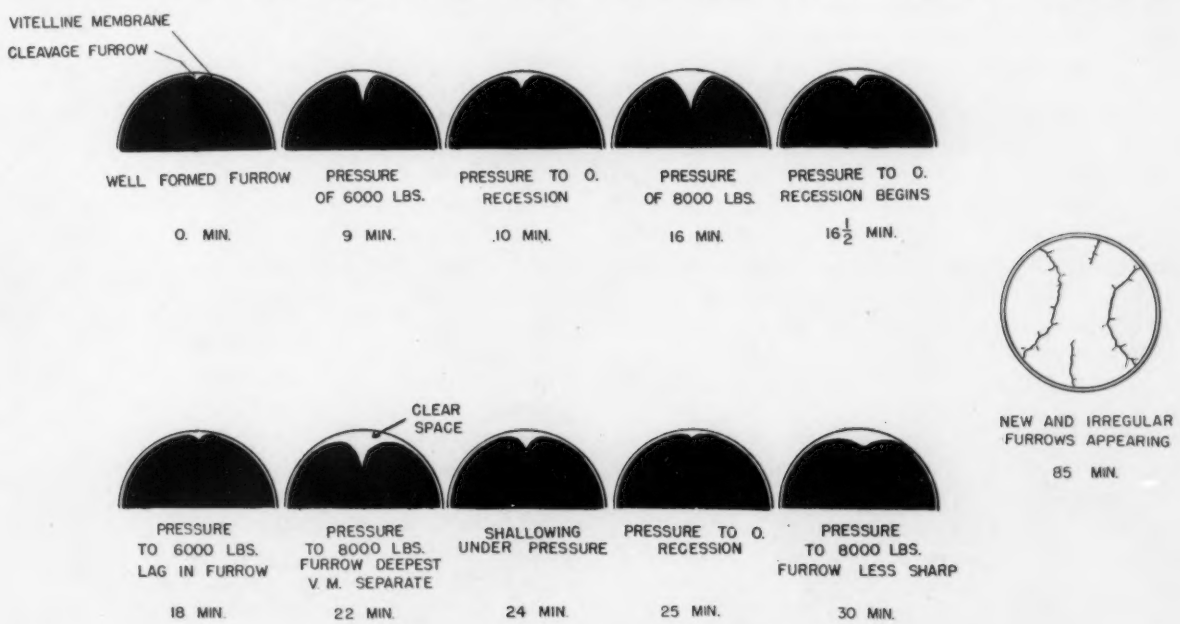


FIG. 2. Cleavage furrow under pressure.

pulling, toward the center of the furrow. As the furrow continued to recede, the tension wrinkles became more numerous and less sharp (no. 4), and soon the entire dorsal surface became involved. Finally, just before the second cleavage began, all of the superficial wrinkling disappeared (nos. 6–8). The second cleavage furrow was generally quite irregular (no. 9), although the tension lines were typical of the normal furrow. Eggs that were compressed late in first cleavage showed a persistence of the surface indications of the first furrow for a longer period (no. 10). Often remnants of the first furrow could be seen while all the succeeding cleavages were being attained. Occasionally only a portion of the first cleavage remained (nos. 11–13). Although the post-pressure cleavages were not generally delayed, they were almost always irregular (nos. 14–16), especially in instances where the pressure was applied during the actual process of furrowing.

Discussion

Until the cytological data of these experiments become available, it is important to emphasize the fact that interpretations of results are based upon macroscopic observations and that such interpretations must, to some extent, be preliminary and tentative.

To interpret the pressure results, it is necessary to keep in mind the normal sequence of developmental events in the frog's egg. The stimulation of fertilization causes a separation of the vitelline membrane from the egg so that gravitational forces rotate the egg into physical equilibrium within 30–40 minutes, at laboratory temperatures. The nuclear material of all uterine eggs (of the frog) is in the metaphase of the second maturation division. While the spermatozoan is making its way into the egg (penetration path), the second polar body is being formed and extruded. This generally occurs from 20 to 30 minutes after insemination. As the haploid egg nucleus re-forms and moves toward the center of the egg, the sperm nucleus veers to meet the egg nucleus (copulation path) at a point between the center of the egg and the center of the animal pole (40–60 minutes). Fusion of the gametes is completed about 1 hour after insemination, at ordinary laboratory temperatures. The cytological details of these and succeeding phases will be presented in a subsequent paper, but it is safe to assume that the nuclear material is being organized for mitosis (*i. e.*, cleavage) from 60 to 120 minutes after the egg is inseminated and that mitotic movements occur immediately thereafter. These terminate in the first cleavage 2½ hours after insemination. The furrow in most eggs is complete by this time, and the mitotic movements for the second cleavage are well under way by 3 hours.

The pressure used (6,000 lb. per square inch) is equivalent to an oceanic depth of approximately 2¼ miles, whereas under normal conditions the eggs of *Rana pipiens* are laid at or near the surface of shallow ponds. Thus the experimental conditions are quite unusual for the frog's egg, although many marine eggs must encounter pressures of a similar magnitude.

It is safe to assume that high hydrostatic pressure in the range employed has no ill effect upon spermatozoa, since it has been shown (Marsland and Rugh, 1940) that frog spermatozoa can be subjected to pressures of 8,000 lb. per square inch, either continuously or via rapidly alternating intervals of compression and decompression, for a period as long as 3 hours without any effect on the motility or the fertilizing power, or on the subsequent role of the sperm nucleus in embryonic development. Further, there is no evidence that the action of the pressure may be primarily upon the egg nucleus as such, although corresponding experiments on the unfertilized egg have not been reported.

The timing of the pressure applications in relation to the serially occurring processes of development appears to be a factor of paramount importance. As may be seen in table 1, very drastic effects are obtained from the earlier applications: (*a*) during membrane elevation and the penetration and migration of the sperm nucleus (4 percent gastrulae, 2 percent tadpoles); (*b*) during polar body extrusion and the approach of the pronuclei (0 percent gastrulae, 0 percent tadpoles); and (*c*) while the pronuclei complete their approach and undergo syngamy (30 percent gastrulae, 16 percent tadpoles). In the intermediate periods: (*a*) after the completion of syngamy and during the migration of the zygote nucleus (90 percent gastrulae, 44 percent tadpoles); and (*b*) while the zygote nucleus remains in the intermitotic condition (70 percent gastrulae, 30 percent tadpoles), the pressure derangement falls to a conspicuous minimum. But in the later periods, when the mitotic and cleavage movements begin to go forward almost without interruption, again the pressure applications give very drastic effects (see table).

At the present time the most tenable interpretation of these results is to consider that pressure interferes primarily with those processes in the egg which have to do with the movements of nuclei and chromosomes whereby these important developmental entities are segregated into the polar body and into the blastomeres. This would explain why the pressure effects are least damaging during syngamy and the inter-mitotic period. Such movements would, of course, be affected by any alteration in the sol-gel equilibria of the egg cortex and other gelated parts of the protoplasm. It is known that pressure of the magnitude used will interfere with: (*a*) spindle formation and chromosome movements (Pease, 1941); (*b*) furrowing and the pinching off of polar bodies; and (*c*) protoplasmic streaming movements generally (Marsland, 1942). Therefore it would seem inevitable that various degrees of heteroploidy might result from the experimental treatment and that drastic developmental derangements should appear subsequently during the critical periods of gastrulation and hatching. These suppositions are borne out by the observations, and the cytological studies which are to follow may help to clarify the hypothesis.

The temporary deepening of the cleavage furrow at the time when the pressure first is applied to the frog's egg is very anomalous and difficult to interpret. Recently Schechtman (1937), utilizing Vogt's method of vitally staining specific areas of the cortex of the egg, concluded that the furrowing of the amphibian egg (*Triturus torosus*) involves a process of cortical gelation. Lewis (1942) and Marsland (1942) also found evidence of cortical gelation and independently reached the conclusion that furrowing in cells generally involves the formation of an equatorial band of gelated cortical protoplasm, which contracts and constricts the cell in two.

In view of the fact that no single exception has yet been found to the general rule that pressure has a solating effect upon protoplasmic gels (Marsland, 1942), the transiently deepened furrow of the compressed frog's egg appears to contradict the other evidence. Of course there are certain gels, for example, gelatin gels (Marsland and Brown, 1941), in which pressure does augment the gelation process. Thus it is not inconceivable that the cortex of the frog's egg represents a gel of this type and that consequently the tension exerted by the constricting furrow actually is increased under pressure. However, this seems far from likely.

Another possible explanation lies in the greater quantity of reserve organic substances, especially lipoids, present in the large yolk-laden frog's egg (McClendon, 1909) as compared with the smaller homolecithal eggs which previously have been studied under pressure. It is known that lipoids generally are more compressible than are aqueous systems,[3] and presumably the bulk of the lipoid material lies internally rather than in the cortex of the frog's egg. Therefore it is probable that the gelated cortex is less compressible and does not suffer as great a volume loss as do the deeper parts under an equivalent pressure. This would mean that under pressure the gelated cortex becomes "too big for" the medullary or inner part of the egg. Under such conditions a temporary deepening of the furrow might occur, even though simultaneously the pressures were inducing a solation of the cortical gel and consequently a reduction in the furrow tension. Further experimental evidence is necessary before a satisfactory decision can be reached. Such experiments will involve the construction of: (1) a larger microscope-pressure chamber, whereby the whole of the frog's egg can be viewed and adequately measured as regards volume changes, and (2) a larger centrifuge-pressure bomb (Brown, 1934), whereby gelation measurements on the cortex of this bigger egg may be obtained. It is probable that the additional data thus obtainable may also give a better basis for understanding the post-pressure recession of the furrows and the simultaneous wrinkling of the cortex, which have been observed in the present experiments.

Summary and Conclusions

1. Hydrostatic pressure (6,000 lb. per square inch) exerts its maximal derangement of the developmental processes of the frog's egg if applied at times when the various nuclear components are undergoing movement and segregation, namely:

(*a*) While the second polar body is being formed and extruded.
(*b*) While the two pronuclei are approaching each other prior to syngamy.
(*c*) During the mitotic movements which lead to the first cleavage.
(*d*) During the actual furrowing of the egg into blastomeres, *i. e.*, during anaphase and telophase changes.

[3] At 10,000 lb. per square inch most aqueous solutions suffer only about 2 percent volume loss, whereas for certain lipoids, at least, the loss is 20 percent.

2. Maximal resistance to this pressure occurs when the pressure is applied during periods when these nuclear components are relatively quiescent, such as:

(*a*) At the completion of syngamy.
(*b*) While the zygotic nucleus is being reorganized for its first mitosis.

3. When cleaving eggs are subjected to this pressure, the furrows deepen during compression but recede subsequent to decompression, disappearing more or less completely within an hour. The recession of the first furrow does not alter the time nor the position of the second furrow. The deepening of the furrow is anomalous compared to many other eggs and may be due to a differential of compressibility in the cortex and in the heavily yolked medulla of the frog's egg.

4. Many of the embryos which hatched, after these experiments, could not be distinguished from those produced by parthenogenetic means, indicating a high incidence of haploidy. This is to be further investigated from a cytological point of view.

5. The tension lines of normal furrowing and of furrow recession can be distinguished, the latter being more in the form of wrinkles occurring at right angles to the original furrow. This post-pressure wrinkling and furrow recession indicate that the pressure produces a marked alteration of the physical properties of the protoplasmic components of the egg, particularly in the egg cortex.

References

Born, G. 1894. Ueber neue Compressionversuche an Froscheiern. *Jahresber. schlesischen Gesell. f. vaterl. Kultur, Zool. Bot.*

Brown, D. 1934. The pressure coefficient of viscosity in the eggs of *Arbacia punctulata*. *Jour. Cell. and Comp. Physiol.* **5**: 335–346.

Conklin, E. G. 1912. Experimental studies on nuclear and cell division in the eggs of *Crepidula*. *Jour. Acad. Nat. Sci. Philadelphia* **15**: 501–591.

Dederer, P. 1910. Pressure experiments on the egg of *Cerebratulus lacteus*. *Arch. f. Entwick. Mech.* **29**: 225–242.

Draper, J. W., and D. J. Edwards. 1932. Some effects of high pressure on developing marine forms. *Biol. Bull.* **63**: 99–107.

Driesch, H. 1893. Zur Verlagerung der Blastomeren des Echinodeneies. *Anat. Anz.* **8**: 348–357.

Hertwig, O. 1893. Ueber den Werth der ersten Furchungeszeelen fur die Organbildung des Embryo. *Arch. mikr. Anat.* **42**: 662–807.

Lewis, W. H. 1942. The relation of the viscosity changes of protoplasm to ameboid locomotion and cell division. In: W. Seifriz (ed.), The structure of protoplasm. Ames, Iowa.

McClendon, J. F. 1909. Cytological and chemical studies of centrifuged frog eggs. *Arch. f. Entwick. Mech.* **27**: 247–258.

Marsland, D. A. 1938. The effects of hydrostatic pressure upon cell division in *Arbacia* eggs. *Jour. Cell. and Comp. Physiol.* **12**: 57–70.

—— 1939. The mechanism of cell division. Hydrostatic pressure effects upon dividing egg cells. *Jour. Cell. and Comp. Physiol.* **13**: 15–22.

—— 1942. Protoplasmic streaming in relation to gel structure in the cytoplasm. In: W. Seifriz (ed.), The structure of protoplasm. Ames, Iowa.

Marsland, D. A., and D. E. S. Brown. 1936. Amoeboid movement at high hydrostatic pressure. *Jour. Cell. and Comp. Physiol.* **8**: 167–178.

—— 1941. The action of pressure on sol-gel equilibria. *Anat. Rec.* **81**: 74 suppl.

Marsland, D. A., and R. Rugh. 1940. Resistance of sperm of *Rana pipiens* to hydrostatic compression; effects upon embryonic development. *Proc. Soc. Exper. Biol. and Med.* **43**: 141–143.

Morgan, T. H. 1893. Experimental studies on echinoderm eggs. *Anat. Anz.* **9**: 141–152.

—— 1910. The effects of altering the position of the cleavage plane in eggs with precocious specification. *Arch. f. Entwick. Mech.* **29**: 205–225.

Pease, D. C. 1941. Hydrostatic pressure effects on the spindle figure and chromosome movement. I. Experiments on the first mitotic division of *Urechis* eggs. *Jour. Morph.* **69**: 405–441.

—— 1942. The inhibition of fertilization and membrane elevation by high hydrostatic pressures. *Jour. Cell. and Comp. Physiol.* **19**: 131–133.

Pease, D. C., and D. A. Marsland. 1939. The cleavage of *Ascaris* eggs under exceptionally high pressure. *Jour. Cell. and Comp. Physiol.* **14**: 407–408.

Pfluger, E. 1884. Ueber die Einwirkung der Schwerkraft und anderer Bedingungen auf die Richtung der Zellthielung. *Arch. gesamte Physiol.* **34**: 607–616.

Regnard, P. 1885. Influence des hautes pressions sur l'éclosion des oeufs de poisson. *C. R. Soc. biol. Paris* **37**: 48–49.

Roux, W. 1885. Beiträge zur Entwicklungsmechanik. III. Ueber die Bestimmung der Hauptrichtungen des Froschenembryo im Ei und über die Erste Teilung des Froscheies. *Breslauer ärztl. Zeitschr.*

—— 1895. Gesammelte Abhandlungen uber Entwicklungsmechanik der Organismen. II. Leipzig.

Rugh, R. 1941. Experimental embryology, a manual of techniques and procedures. New York.

Schechtman, A. M. 1937. Localized cortical growth as the immediate cause of cell division. *Science* **85**: 222–223.

Wilson, E. B. 1896. On cleavage and mosaic work. *Arch. f. Entwick. Mech.* **3**, appendix: 19–26.

Yatsu, N. 1910. Experiments on germinal localization in the egg of *Cerebratulus*. *Jour. Coll. Sci. Tokyo* **27**: 1–32.

Ziegler, H. E. 1894. Ueber Furchung unter Pressung. *Verh. anat. Gesell.* **8**: 132–146.

A CANCEROUS NEOPLASM OF PLANTS PRODUCED BY AUTONOMOUS, BACTERIA-FREE CROWN-GALL TISSUE

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(*Read April 24, 1942*)

IN ANY analysis of those characteristics of complex living organisms which are of fundamental importance for their survival and general well-being, one is struck forcibly by the extraordinary way in which all functional parts fall into a coherent, flexible, but definitely limited pattern. This characteristic is so ubiquitous that it is likely for the most part to be passed over unnoticed.

Sometimes, however, this harmony of structure and function is abruptly brought to our attention by its sudden failure. This is never more true than in the disease which we call "cancer," for here the significant feature of the disease is the breakdown of morphogenetic control, the failure of the diseased cells to respond to the restraints which direct their growth in healthy organisms. The invasiveness, the malignancy, the capacity to move from the primary focus to other foci as metastases and to permit transplantation from one organism to other related organisms without loss of malignancy are all, so far as the cell itself is concerned, expressions of this fundamental irresponsibility. The affected cells have become anarchists, no longer obeying the laws of well-ordered society.

In animal cancer this quality is acquired in some unknown fashion and, once acquired, is retained indefinitely without obvious proximate cause. Tumefactions of plants having the appearance and behavior of cancers have, so far as they have been studied previously, all differed from animal cancers in possessing a demonstrable cause in the form of some one or more invading organisms.

We propose to discuss here a tumefaction of plants which continues to behave in the irresponsible manner characteristic of malignant tumors after elimination of the original causal agent. We believe that, in all fundamental respects, this tumefaction is a true cancer.

When sunflower seedlings are inoculated just above the cotyledons by single pricks of a needle dipped in a suspension of gall-producing bacteria of the species *Phytomonas tumefaciens*, there arise rapidly developing tumors which may reach the size of a small orange. The tissues of the tumors are disorganized, invasive, and sometimes malignant, and are capable of producing similar tumors when transplanted elsewhere in the same or in other hosts. The galls are, however, not truly autonomous, since bacteria can always be isolated from them. Some weeks after inoculation there frequently appear, in the neighborhood of the vascular bundles for a distance of one or more internodes above the primary tumors, numerous small swellings connected by strands of modified host tissue. These are known as "tumor strands." It has usually been assumed that they arose as a result of small numbers of bacteria migrating or being drawn through the conducting vessels or intercellular spaces of the host to distant points. Bacteria can sometimes be isolated from such tumor strands. In addition to the primary tumors and tumor strands, characteristic swellings appear in a considerable percentage of cases on the petioles and large veins and especially just at the bases of the petioles of leaves to a distance of 3 or 4 nodes above the primary tumors. These are called "secondary tumors." Out of 181 such distant secondary tumors tested carefully in recent months by a variety of proven bacteriological methods, only 7—or about 4 percent—yielded cultures of crown-gall bacteria. They are typically bacteria-free.

The fact that galls arise at these isolated points is a demonstration that the local tissues are in an abnormal condition and are growing much more rapidly than are the adjacent unaffected tissues. Fragments excised from such galls have been cultivated *in vitro* as tissue cultures as a means of studying their properties. These studies have brought to light very interesting and, we believe, important facts.

Normal sunflower cells in tissue culture grow very slowly. The cultures retain a smooth outer surface. They are usually green in color and

often develop roots as might any cutting. Internally they form well-organized woody xylem which renders them fibrous and hard in texture. Cultures maintained for almost a year have in that time increased in volume only about 250-fold. By contrast, tissue cultures isolated from secondary crown-gall tumors have in a corresponding period increased in volume more than a million million fold. They are glistening white in color, except for occasional brown patches of dead, necrotic cells. They never form roots. The surface is covered with numberless minute tubercles representing localized centers of more rapid growth. They are firm but not woody or fibrous, friable, and, although they contain scattered scalariform cells, these are not organized into any coherent system. The marked difference in behavior of tumor tissue and healthy tissue is worth emphasizing. Healthy tissues, even under the simplified conditions of tissue cultures, continue to respond to certain morphogenetic restraints typical of the intact organism. Tumor tissues, on the other hand, under the same conditions override these restraints and behave in the anarchistic manner typical of cancer cells. We have subjected about 600 such cultures to careful bacteriological tests without ever recovering crown-gall bacteria from them. We have subjected them to serological tests, immunizing rabbits against tumor tissue cultures and then carrying out agglutination and complement fixation tests using broth cultures of crown-gall bacteria as antigen without detecting any trace of evidence of bacteria in the original tissues. We have grown more than 1,000 tumor-tissue cultures in contact with a nutrient known to support growth of these bacteria without ever isolating colonies therefrom. From this and other evidence, it is necessary to conclude that these tissues and the tumors from which they were derived were devoid of the bacteria whose presence elsewhere in the host was responsible in some as yet unknown way for the original tumefaction.

The capacity of animal tumors to metastasize —to move from the primary focus to new and distant foci in the original host, or to be transplanted to new foci in related hosts where they produce new tumors—is a characteristic result of morphogenetic anarchy. When fragments of healthy sunflower tissue—pith, or wood, or young growing points, or tissue cultures of healthy tissue—are implanted under the bark of young healthy sunflower plants as "grafts," they frequently "take," fusing with the host tissues, becoming vascularized and continuing to grow. Such healthy tissue grafts are subject to the same morphogenetic restraints as are the tissues of the host itself and soon fall into the normal pattern, stock and scion becoming indistinguishable. When, on the other hand, instead of healthy tissues, living fragments of bacteria-free tissue cultures from secondary crown-gall tumors are implanted, a very different picture emerges. If the fragments are so placed that a vascular connection to the host becomes established, the grafts quickly develop into typical crown-gall tumors. From about 600 such grafts carried out during the past year, we have obtained 133 unmistakable tumors ranging in size from nodules a few millimeters across to some the size of a walnut. Successful grafts have been made from tissue cultures derived from 11 different tumors. The tumor-forming capacity is, therefore, a general characteristic of excised tumor tissue. Some of the tissues producing tumors had previously been carried in culture for more than a year, through 25 successive passages. The tumors arose mostly by increase of the implanted fragment and only to a minor extent from host tissues. They were induced only by tumor implants which were themselves capable of growth —when the implant was first ground thoroughly it no longer produced a tumor. This is additional evidence that the tissues used did not contain crown-gall bacteria, since bacteria-bearing primary gall tissue similarly treated regularly produces huge, rapidly growing galls. It is also presumptive evidence against the involvement of a tumefacient virus. The tumor cells themselves had become disease-producing agents.

The evidence presented shows that, under the indirect influence of crown-gall bacteria originally present in some distant part of the plant, certain tissues of sunflower seedlings lose their characteristic behavior, cease to respond to normal morphogenetic restraints, acquire a capacity for greatly accelerated and disorganized growth, and thus produce invasive and potentially malignant tumors. This new behavior becomes an intimate function of the cells themselves, independent of any continued bacterial stimulation, so that the affected tissues can be removed from the host, cultivated *in vitro* for long periods as bacteria-free tissue cultures of rapid growth and disorganized habit, and on re-implantation into new hosts of the same or related species, give

rise to new tumors indistinguishable from those from which the cultures were originally derived. The tumor cells have become autonomous, parasitic, and malignant. Tumefactions can be produced at will, and evidence is available which suggests that it may be possible to follow step by step the processes by which the affected cells take on this new behavior.

These characteristics have not previously been demonstrated convincingly in any other plant material. They are, so far as the affected cell is concerned, the same characteristics as those by which animal cancers are distinguished from healthy or merely inflammatory animal tissues. The material seems to be extremely promising for the investigation of those fundamental cellular changes which are the biological bases of "the cancer problem."

POTATO WITCHES'-BROOM TRANSMISSION BY DODDER AND CURE BY HEAT

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A DISEASE known as witches'-broom occurs in potato fields of Maine (Folsom and Bonde, 1936) and other northern states. It also occurs in Canada (Eastham, 1928), China (Yu, 1939), Italy (Cristinzio, 1935), Scotland (Murphy and M'Kay, 1932), Ireland (Clinch, Loughnane, and Murphy, 1938), Poland (Ruszkowski, Zweigbaumówna, and Blockówna, 1938), and Russia (Jaczewski, 1926). It probably occurs in a number of other countries. Witches'-broom is a disease of great severity but one that usually is of minor economic importance because of low incidence. However, in Montana and other northwestern states (Brentzel, 1935; Young and Morris, 1928), where in some years it affects large numbers of plants, it has been destructive.

Witches'-broom has not been transmitted mechanically by means of juice. It is known to pass from crop to crop through tubers and has been transferred to healthy potato and tomato plants by grafting (Young, 1927). In potato fields it presumably is spread by one or more insects, but no insect vector has yet been discovered. The disease was adequately described by Hungerford and Dana (1924) and by Young and Morris (1928). It is a typical witches'-broom and belongs in the yellows group of virus maladies.

The writer is indebted to Dr. Donald Folsom, of the Maine Agricultural Experiment Station, for the sample of virus used in the experiments to be reported. Early symptoms of the disease as it developed in the greenhouses at Princeton, New Jersey, consisted in a yellowing and rolling of leaves. Aerial tubers, stolons, and other types of secondary shoots were produced in large numbers. Many of the aerial stolons resembled roots to a remarkable degree. They were as slender as roots, reacted to gravity like roots, and bore trichomes that resembled root hairs. This is shown by the photograph presented in figure 1. Since a number of different virus diseases in the yellows group had been cured by heat (Kunkel, 1936, 1941, 1942), it was decided that the heat-treatment method should be tried on witches'-broom. The main purpose of this paper is to report the results obtained.

EXPERIMENTAL

The potato plant cannot endure high temperatures for long periods of time. Therefore, it was desirable to take the disease to a plant that would be more suitable for use in heat-treatment experiments. *Vinca rosea* L., a native of Madagascar, was available and was known to be heat-enduring.

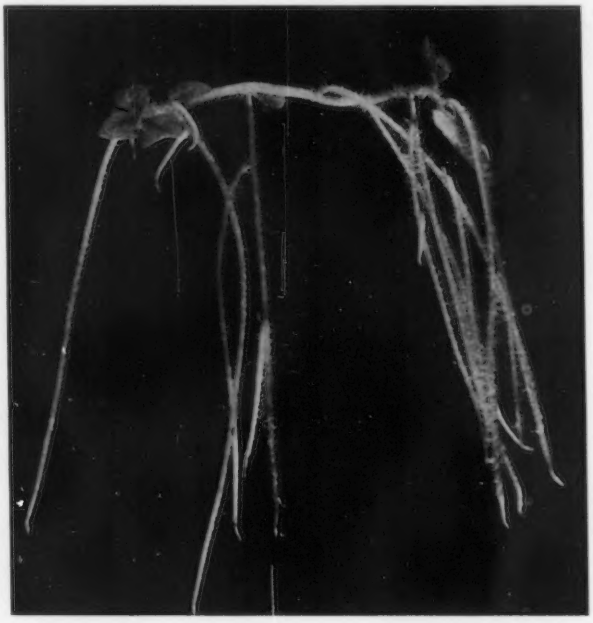

FIG. 1. Aerial stolons from a witches'-broom potato plant of the variety Katahdin. Trichomes on the stolons resemble root hairs. (Photograph by J. A. Carlile.)

It was not known to be susceptible to witches'-broom, and its susceptibility could not be tested by means of graft inoculations because it could not be successfully grafted with the potato. Since dodder (Bennett, 1940; Johnson, 1941) had been used to transmit several plant viruses that could not be passed by means of juice, it offered a possible means of taking witches'-broom to *V. rosea*.

Experiment 1

In the first test, dodder of the species *Cuscuta campestris* Yuncker that had grown on witches'-

broom potato plants for several weeks was placed on 3 healthy young potato plants. Dodder that had grown on healthy tomato plants for a like period of time was placed on 3 other healthy potato plants that served as controls. The 3 plants exposed to dodder from the witches'-broom potato plants came down with witches'-broom about a month after exposure. The control plants remained healthy. The experiment showed that dodder was capable of transmitting witches'-broom virus.

Experiment 2

In this experiment, dodder that had developed on witches'-broom potato plants was placed on each of 12 healthy young *Vinca rosea* plants. It also was placed on 5 plants of each of the following species: *Nicotiana glutinosa* L., *N. rustica* L., tomato, and sugar beet. Dodder from healthy tomato plants was placed on each of 3 other healthy young *V. rosea* plants and on 3 *N. glutinosa* plants, 3 *N. rustica* plants, 3 tomato plants, and 3 sugar beet plants that were to serve as controls. In from 1 to 3 months, 11 of the 12 *V. rosea* plants that were exposed to witches'-broom dodder came down with a yellows type of disease that was presumed to be witches'-broom. Likewise, the *N. glutinosa*, *N. rustica*, tomato, and 2 of the 5 sugar beet plants that were exposed to witches'-broom came down with a witches'-broom type of disease. All control plants remained healthy. The experiment showed that *V. rosea*, *N. glutinosa*, *N. rustica*, tomato, and sugar beet plants were susceptible to witches' broom virus.

Experiment 3

The next experiment was made for the purpose of determining whether the disease transmitted to *Vinca rosea* would cause symptoms typical of witches'-broom when taken back to the potato. Dodder from healthy tomato plants was placed on 2 diseased *V. rosea* plants. After growing on the plants for about a month, several branches were transferred to 3 healthy young potato plants. At the same time dodder from a healthy *V. rosea* plant was transferred to 3 other healthy young potato plants that served as controls. All of the 3 plants on which dodder from diseased periwinkles was placed came down with typical witches'-broom. The control plants remained healthy. The experiment proved that the disease taken to *V. rosea* by means of dodder was potato witches'-broom. It was concluded that the disease taken to the other species also was witches'-broom.

Experiment 4

In a further transmission experiment, witches'-broom was taken to 31 out of 36 *Vinca rosea* plants exposed to dodder from diseased *V. rosea* plants. It also was transmitted to about 50 healthy *V. rosea* plants by grafting. The experiment showed that witches'-broom could be transmitted readily from diseased to healthy *V. rosea* plants both by dodder and by grafting. In addition, it furnished an ample supply of diseased periwinkle plants suitable for use in heat-treatment experiments.

Experiment 5

In the first heat-treatment experiment, 25 diseased *Vinca rosea* plants were placed in a hot room held at 42° C. Five other diseased *V. rosea* plants that served as controls were kept in a greenhouse held at a temperature of about 25° C. Five plants were transferred from the hot room to the greenhouse in which the controls were kept after each of the following intervals: 9, 11, 13, 15, and 17 days. All plants were held under observation for a period of 8 months from the time they were placed in the greenhouse. The new growth produced by all of the treated plants during this period appeared to be healthy, except shoots that developed on the stems of some of the plants near the ground level. After from 1 to 3 months, all of the plants treated for 9 and 11 days produced diseased shoots near the ground. This showed that their underground parts had not been cured. The plants treated for 13, 15, and 17 days showed no symptoms of disease during the 8-month period. The check plants showed typical symptoms at all times. It was concluded that the plants treated for 13, 15, and 17 days had been cured. One of the cured plants and a diseased control plant are shown in figure 2.

Experiment 6

Since the tops of all of the treated plants described in Experiment 5 were apparently cured, it was decided to test the curative action of shorter treatments. Six sets of 5 diseased *Vinca rosea* plants each were placed in a hot room at 42° C. One set was removed after each of the following intervals: 2, 3, 4, 5, 6, and 7 days. A seventh set

FIG. 2. Cure of potato witches'-broom in *Vinca rosea*. Witches'-broom was transmitted to both plants at the same time by dodder. Five and a half months later both were equally diseased when the plant on the left was given a heat treatment at 42° C. for 17 days. The picture was taken 4 months after the treatment and shows that the treated plant was cured. (Photograph by J. A. Carlile.)

that was not treated served as a control. The plants held in the hot room for 2 days showed symptoms of witches'-broom in the new growth that developed after treatment. They were similar to the control plants in every respect. New growth that developed in the tops of all other treated plants was healthy. However, in from 1 to 2 months after treatment all of the plants showed symptoms of witches'-broom in shoots produced near the ground level. It was concluded that treatments at 42° C. for 2 days had produced no appreciable effect on the plants. Treatments for 3, 4, 5, 6, and 7 days cured the tops but not the roots.

Experiment 7

It also was decided to test the effectiveness of a lower temperature than 42° C. The temperature chosen was 36° C. Five sets of 5 diseased *Vinca rosea* plants each were held in a hot room at 36° C. for 5, 7, 9, 11, and 13 days, respectively. Five other diseased plants that were not treated served as controls. All plants were held under observation for 8 months. The new growth produced by the plants treated for 7, 9, 11, and 13 days was healthy in appearance. That produced by the plants treated for only 5 days showed symptoms of witches'-broom. About a month after treatment most of the plants with healthy-appearing tops bore diseased shoots near the ground level. Within 3 months after treatment all bore such shoots. The control plants showed witches'-broom symptoms throughout the period. It was concluded that neither the tops nor the underground parts of plants treated for 5 days at 36° C. were cured. The tops but not the roots of plants treated for 7 days or longer were cured.

Experiment 8

When the information yielded by the heat-treatment experiments with *Vinca rosea* became available, an attempt to cure witches'-broom in potato tubers was planned. It was hoped that the tubers could be cured by treatments that would cause little or no injury. Experience gained in curing witches'-broom in *V. rosea* seemed to justify the belief that small tubers might be cured by a treatment employing 36° C. for as short a period as 6 days. Experiment 8 was made to test this possibility. The only witches'-broom tubers at hand were small. None was more than ¾ inch in diameter. A dozen of these small tubers were placed in each of two 8-inch clay saucers. One saucer was placed in a hot room held at 36° C.; the other was placed in a greenhouse where the temperature was about 25° C. After 6 days of treatment, half of the tubers in each saucer were planted in soil in 6-inch pots. The pots were placed in a cool greenhouse. All of the 6 tubers held in the hot room produced healthy-appearing vines that grew to be as large as could be expected of plants in 6-inch pots. They yielded a total of 35 tubers having diameters ranging from 1¼ to a little more than 2 inches. The 6 untreated tubers planted at the same time each produced a few thin, diseased vines and yielded no tubers whatever. The other 12 tubers were not planted. The experiment proved that witches'-broom in potato tubers could be cured and that for small tubers a treatment at 36° C. for 6 days was sufficient.

Experiment 9

When it was learned that a temperature of slightly less than 97° F. (36° C.) cured the tops of *Vinca rosea* plants in 7 days and small potato tubers in 6 days, it was surmised that summer temperatures, especially in greenhouses, might be high enough to benefit witches'-broom plants. In a test of this hypothesis, 5 diseased potato plants, 5 diseased tomato plants, and 5 diseased *V. rosea* plants were placed in a greenhouse where the temperature exceeded 97° F. for considerable periods during the hours of daylight. At the same time 5 other diseased plants of each species were placed in a greenhouse where the temperature was held below 90° F. at all times by running cold water over the glass. After 3 weeks a marked improvement was noted in the appearance of all plants in the high-temperature house. There was little or no improvement in the appearance of the plants in the low-temperature house. A tomato and a *V. rosea* plant from the high-temperature house are presented in figures 3 and 4, respectively. The picture of the tomato was taken on June 17, when the plant showed an early stage of the partial recovery that occurred. The tomato had been diseased since the previous January. The badly stunted lower branches that bore curled leaves developed dur-

FIG. 3. A tomato plant showing partial recovery from potato witches'-broom owing to the beneficial action of high summer temperatures. (Photograph by J. A. Carlile.)

FIG. 4. A *Vinca rosea* plant showing considerable recovery from potato witches'-broom as a result of the curative effects of high summer greenhouse temperatures. (Photograph by J. A. Carlile.)

ing the winter months when greenhouse temperatures varied between 70° and 80° F. The two branches forming the upper part of the plant were produced in the high-temperature greenhouse. It will be seen that the leaves borne by these branches were almost normal in appearance. The *V. rosea* plant was photographed on July 24. It had been in the high-temperature greenhouse a little more than 8 weeks and showed an advanced stage of recovery. The portions of branches in the lower and central part of the plant bore fine shoots and narrow leaves that are characteristic of witches'-broom. They were produced during the winter months while the plant was held at 70° to 80° F. The tips of these branches bearing normal flowers and leaves were produced in the high-temperature greenhouse. It was thought that the healthy-appearing tips might be virus-free, but when some were cut off and rooted in sand, they produced diseased plants. This proved that, although they appeared to be healthy, they were not free of witches'-broom virus. The experiment showed that diseased potato, tomato, and *V. rosea* plants were benefited by the high temperature that prevailed in an uncooled greenhouse during June and July.

DISCUSSION

Witches'-broom of potato is the first potato virus disease and the ninth plant virus disease to be cured by heat. The treatment employed caused no perceptible injury to tubers such as were produced by diseased plants grown in 6-inch pots in greenhouses. It is probable that in potato fields some virus-carrying tubers of normal size are produced. These no doubt would require a somewhat longer treatment than was necessary for small tubers. However, it seems probable that even large tubers can be cured by relatively mild treatments and that the heat-treatment method may prove to be of some value as a means of control. The improvement observed in the condition of diseased potato, tomato, and *Vinca rosea* plants during summer months suggests that the witches'-broom virus would not flourish in a hot climate. The improvement probably resulted from inactivation of a considerable portion of the virus present in the tissues. No attempts were made to cure witches'-broom in tomato, potato, *Nicotiana glutinosa*, *N. rustica*, or sugar beet plants. It was cured in *V. rosea* by treatments that caused only a slight injury to some of the youngest leaves.

Nothing is known regarding a relationship between witches'-broom and other plant virus diseases of the yellows group. In respect to thermal inactivation *in vivo*, witches'-broom virus reacts much like that of aster yellows. It is more resistant to heat than peach yellows virus (Kunkel, 1936) but less resistant than peach rosette (Kunkel, 1936) or cranberry false-blossom virus (Kunkel, 1942). The disease in *Vinca rosea* could not be distinguished from either aster yellows or cranberry false blossom. It also closely resembled these diseases in the tomato. The fact that it went to sugar beet plants that are immune from aster yellows indicated that it was not closely related to this disease and confirmed the conclusion reached in an earlier study (Kunkel, 1928).

Little is known at present regarding the host range of witches'-broom. The discovery that it can be transmitted by dodder offers a means of testing the susceptibility of any species that may be selected for investigation. Future studies on host range may throw light on any relationships

that exist between witches'-broom and other virus diseases of the yellows type.

Summary

(1) Potato witches'-broom virus was transmitted to *Nicotiana glutinosa*, *N. rustica*, tomato, sugar beet, and *Vinca rosea* by the dodder, *Cuscuta campestris*.

(2) The disease caused in *Vinca rosea*, a high-temperature plant, was cured by heat. Treatments at 36° C. for 5 days did not cure either the tops or the roots of potted plants. Treatments at 36° C. for 7 days or at 42° C. for 3 days cured the tops but not the roots. Treatments at 42° C. for 13 days or longer cured both the tops and roots.

(3) Potato tubers having diameters up to ¾ inch were cured by treatments at 36° C. for 6 days.

(4) Potato, tomato, and *Vinca rosea* plants were benefited but not cured by summer greenhouse temperatures that exceeded 97° F. for considerable periods during daylight hours. They were not noticeably benefited by summer greenhouse temperatures that were held below 90° F. at all times.

Literature Cited

Bennett, C. W. 1940. Acquisition and transmission of viruses by dodder (*Cuscuta subinclusa*). (Abst.) *Phytopathology* **30** (1): 2.

Brentzel, W. E. 1935. Types of potato virus diseases in North Dakota. *Bull. North Dakota Agric. Exper. Sta.* 282: 1–23.

Clinch, P., J. B. Loughnane and P. A. Murphy. 1938. A study of the infiltration of viruses into seed potato stocks in the field. *Sci. Proc. Royal Dublin Soc.*, n.s. **22**, paper 2: 17–31.

Cristinzio, M. 1935. [The virus diseases of Neapolitan "Riccia" and "Biancona" potatoes in the year 1934.] *Ric. Ossvz. Divulg. Fitopat. Campania ed Mezzogiorno Portici* **4**: 51–65.

Eastham, J. W. 1928. Report of Provincial Plant Pathologist, Vancouver. *22nd Ann. Rept. Dept. Agric. British Columbia 1927:* Q34–Q37.

Folsom, D., and R. Bonde. 1936. List of distinct potato viroses. *Am. Potato Jour.* **13**: 14.

Hungerford, C. W., and B. F. Dana. 1924. Witches' broom of potatoes in the Northwest. *Phytopathology* **14** (8): 372–383.

Jaczewski, A. A. 1926. [Witches' broom of the potato.] *Mater. Mikol. i Fitopat.* **5** (2): 117–128. [In Russian. Abst. in *Rev. Appl. Mycol.* **6**: 746, 1927.]

Johnson, F. 1941. Transmission of plant viruses by dodder. *Phytopathology* **31** (7): 649–656.

Kunkel, L. O. 1928. Further studies on the host range of aster yellows. (Abst.) *Phytopathology* **18** (1): 156.

—— 1936. Heat treatments for the cure of yellows and other virus diseases of peach. *Phytopathology* **26** (9): 809–830.

—— 1941. Heat cure of aster yellows in periwinkles. *Am. Jour. Bot.* **28** (9): 761–769.

—— 1942. False blossom in periwinkles and its cure by heat. *Science* **95**: 252.

Murphy, P. A., and R. McKay. 1932. A comparison of some European and American virus diseases of the potato. *Sci. Proc. Royal Dublin Soc.*, n.s., **20**, paper 27: 347–358.

Ruszkowski, J., Z. Zweigbaumówna, and H. Blockówna. 1938. [Diseases of cultivated plants in Poland in 1937.] *Roszn. Ochr. Rosl.* **5** (4): 49–102.

Young, P. A. 1927. Transmission of potato witches' broom to tomatoes and potatoes. *Science* **66** (1709): 304–306.

Young, P. A., and H. E. Morris. 1928. Witches' broom of potatoes and tomatoes. *Jour. Agric. Res.* **36** (10): 835–854.

Yu, T. F. 1939. A list of plant viroses observed in China. *Phytopathology* **29** (5): 459–461.

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